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Global litter production, pools, and turnover times: Estimates from measurement data and regression models

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Abstract. Systematic and compatible databases to quantify composition, distribution, and turnover times of carbon in global litter were developed and evaluated. The study employs an integrated approach, estimating related litter pools and fluxes using a variety of data-based and model-based techniques. The analysis includes direct estimates and indirect, or proxy, estimates of litter production and pools; steady-state turnover times are estimated from the two. Proxies for litter production include net primary productivity and root respiration-soil respiration relationships. In addition to implementing a suite of regression models, >1100 published measurements of litter components, along with site characteristics, were integrated into a baseline data set and used to estimate litter production and pools. Historically, global estimates of litter production have ranged from 75 to 135 Pg dm/yr; several estimates from this study suggest values in the middle of this range, from 90 to 100 Pg dm/yr. The estimate of aboveground litter production from the compiled measurements, 39 Pg dm/yr, includes mainly forest, woodland, and wooded grassland; other grassland, shrubland, and xeromorphic communities that occupy ~25% of the ice-free land surface are unrepresented in the present compilation. Aboveground litter production may be 5-10 Pg dm/yr higher with the inclusion of these ecosystems, and the total, including belowground production, may approach 90-110 Pg dm/year. Two novel production estimates derived from soil- and root-respiration relationships are 93 Pg and 100 Pg dm/yr. These estimates have the major advantage of accounting for both aboveground and belowground litter; the latter is rarely included and can account for a substantial fraction of total production. Production of coarse woody detritus may add ~12 Pg dm/yr to the fine litter total. The global litter pool has previously been estimated at ~100 to 400 Pg dm. The fine litter pool estimated here from the measurement compilation is 136 Pg dm. Although this partial estimate includes ecosystems covering just under half the ice-free land surface, it encompasses forests and woodlands which have the largest pools. Inclusion of the remaining ecosystems may add ~25 Pg, raising the total to ~160 Pg dm. An additional ~150 Pg dm is estimated for the coarse woody detrital pool. Global mean steady state turnover times of litter estimated from the pool and production data range from 1.4 to 3.4 years; mean turnover time from the partial forest/woodland measurement compilation is ~5 years, and turnover time for coarse woody detritus is ~13 years. By encompassing spatial distribution, composition, and magnitude, along with numerous field measurements, this integrated approach has begun to yield compositional and ecosystem constraints on modeled global and regional litter fields and NPP allocation schemes in ecosystem models.

1. Introduction

A broad spectrum of carbon cycle models focuses on characteristics of biospheric pools and fluxes at a variety of temporal scales ranging from seasons [e.g., *Pearman and Hyson*, 1981; *Fung et al.*, 1983, 1987; *Kohlmaier et al.*, 1987; *Potter et al.*, 1993] to centuries and millennia [e.g., *Jenkinson and Raynor*, 1977; *Parton et al.*, 1987, 1988; *Adams et al.*, 1990; *Prentice and Fung*, 1990; *Friedlingstein et al.*, 1992, 1995; *Schimel et al.*, 1994]. Attempts to explain equilibrium and transient responses to natural and anthropogenic perturbations of nutrient pools and fluxes suggest that responses vary with climate, ecosystem, and mode of disturbance and that the carbon pools involved depend on the time scales of the perturbations [e.g., *Martel and Paul*, 1974; *Martel and MacKenzie*, 1980; *Goudriaan and Ketner*, 1984; *Alegre and Cassell*, 1986; *Mann*, 1986; *Zielke and Christenson*, 1986; *Esser*, 1987; *Parton et al.*, 1987; *Burke et al.*, 1989; *Blank and Fosberg*, 1989; *Post and Mann*, 1990; *Dai and Fung*, 1993; *Kirschbaum*, 1993; *Schindler and Bayley*, 1993; *Hudson et al.*, 1994; *Schimel et al.*, 1994; *Townshend et al.*, 1992, 1994].

Quantification of steady state and transient carbon exchanges among the atmosphere, oceans and biosphere requires inventories and turnover times of components of the carbon cycle [e.g., *Tans et al.*, 1993; *Fung*, 1993; *Ciais et al.*, 1995]. Some terrestrial ecosystem and biogeochemistry models that predict biospheric state and behavior under equilibrium or transient conditions rely, for carbon pool sizes, fluxes, and turnover times, on general ecosystem composites [e.g., *Whittaker and Likens*, 1975; *Ajtay et al.*, 1979; *Raich and*

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Schlesinger, 1992] or on data modeled directly from climate or via climate-derived distributions of vegetation [*Lieth*, 1975; *Esser et al.*, 1982; *Esser*, 1987; *Esser and Lieth*, 1989; *Post et al.*, 1982, 1985; *Prentice and Fung*, 1990; *Friedlingstein et al.*, 1992; *Dai and Fung*, 1993; *Foley*, 1994, 1995; *Bonan*, 1995]. Other models that rely on stable isotopes ($^{13}C/^{12}C$) to constrain the carbon budget require information on composition, age, and isotopic signatures of respired biospheric carbon [e.g., *Quay et al.*, 1991; *Tans et al.*, 1993; *Fung*, 1993; *Ciais et al.*, 1995]. In addition, ^{14}C measurements and modeling applied to analyzing the rapidity and magnitude of carbon cycling at individual sites require techniques and data bases to extrapolate results globally [*Trumbore et al.*, 1989, 1990; *Trumbore*, 1993; *Harrison et al.*, 1993].

During the last decade, efforts have focused on understanding controllers of carbon exchange in order to reduce uncertainties in evaluating the role of the biosphere during the last several decades as a carbon sink or source, as well as potential changes in carbon balance in response to climate changes [*Pastor and Post*, 1988; *Post*, 1990; *Prentice and Fung*, 1990; *Jenkinson et al.*, 1991; *Gorham*, 1991; *Shaver et al.*, 1992]. The large ranges observed in litter characteristics within and among ecosystems, along with the variety of biotic and abiotic parameters correlated with carbon inputs and pools, has lead to substantial discrepancies among estimates of litter production, pools, and turnover times which are further reflected in terrestrial ecosystem models. These ranges can be large if relying on different modeling approaches and data, or misleadingly small if models rely on the same data sets for development, initialization, and testing.

Estimates of the global litter pool range from a low of ~100-150 Pg dm (1 Pg = 10^{15} g; dm = dry matter) [*Whittaker and Likens*, 1975; *Schlesinger*, 1977; *Goudriaan and Ketner*, 1984; *Ajtay et al.*, 1979; *Rotmans and DenElzen* 1993; *Hudson et al.*, 1994; *Friedlingstein et al.*, 1995] to a high of ~300-400 Pg dm [*Esser et al.*, 1982; *Esser*, 1987; *Potter et al.*, 1993; *Foley*, 1994] using a variety of extrapolation and modeling techniques (Table 1a). Causes underlying these discrepancies are difficult to identify. While information about the geographic distribution of litter pools is sometimes provided explicitly [*Esser et al.*, 1982; *Foley*, 1994, 1995], most results are reported for the globe or as ecosystem means, allowing only general evaluation and comparison with other distributions. Some of the variation may be due to differences in the definition of litter. Components of the litter pool are frequently unexplained and few of the estimates include coarse woody detritus (usually >7 cm diameter) [Harmon et al. 1986] or reflect underground detritus. For most production values it is difficult to determine what part of fine woody litter is included. Litter pool measurements exhibit greater scarcity although some suggest that including standing and fallen dead wood may increase estimates of the fine litter pool by ~40% [*Ajtay et al.*, 1979].

The potential effects of mobilizing such a pool in response to sustained climate change (e.g., warming and drying) is substantial. Moreover, climatic modulation of production and decomposition dynamics may initiate sequestration or loss of organic matter in litter and labile soil pools thereby influencing interannual variations in ecosystem carbon balances and atmospheric CO_2 concentrations [*Trumbore*, private communication, 1995; *Dai and Fung*, 1993]. Finally, there is no in-depth evaluation of the global distribution of coarse woody detritus [*Harmon et al.*, 1986, 1993; *Harmon and Hua*, 1991] although it may be as large as the fine litter pool but with a longer turnover time.

In contrast to the litter pool, a variety of direct and indirect extrapolation and modeling techniques for estimating annual litter production converge in the range of 75-135 Pg dm [e.g., *Ajtay et al.*, 1979; *Reiners*, 1973; *Whittaker and Likens*, 1975; *Esser et al.*, 1982; *Meentemeyer et al.*, 1982; *Fung et al.*, 1983; *Goudriaan and Ketner*, 1984; *Esser*, 1987; *Rotmans and DenElzen*, 1993] (Table 1b). Estimates of the major input to litter production (i.e., net primary production) and the dominant short-term disposition of litter production (i.e., soil respiration) are generally consistent with the lower range [*Lieth*, 1975; *Box*, 1988; *Dai and Fung*, 1993; *Melillo et al.*, 1993; *Foley*, 1994; *Hudson et al.* 1994; *Ruimy et al.*, 1994; *Warnant et al.*, 1994; *Bonan*, 1995].

In order to examine patterns of litter distribution and turnover including variations within and among ecosystems, we compiled a large number of measurements of production, pools, and turnover into an internally consistent global database. The study employed an integrated approach evaluating related carbon pools and fluxes using a variety of data-based and modeled-based techniques. The analysis includes direct estimates and indirect, or proxy, estimates; steady-state litter turnover times are estimated from the pool and production data.

Section 2 provides definitions and a description of the approaches and the data used in the study. Results of a suite of litter production estimates are presented in Section 3 and those for litter pools in Section 4. Section 5 examines litter turnover times estimated from pools and production. Uncertainties are discussed in Section 6. Conclusions and perspectives are presented in Section 7.

2. Definitions, Approaches, and Data

2.1. Definitions

Definitions of litter production (also referred to as litterfall and detrital production) and litter pool (forest floor mass or littermass) differ among authors and applications. The term litter pool is rarely well defined partly because it is inherently difficult to determine in the field. In addition, the transition between surface materials and underlying material in increasing states of decay is gradual, so that the distinction between litter and soil organic matter (SOM) is less than exact. For this study, litter pool is defined as "recently fallen litterfall and decomposing organic matter above the mineral soil" [*Vogt et al.*, 1986, p. 305]. Note that surface detritus or litter pool is sometimes included with soil carbon as in the model of *Meentemeyer et al.* [1985], although it is not included in *Post et al.'s* [1982, 1985] soil carbon profiles. The difficulty in distinguishing between partially decomposed material of the surface litter pool and SOM is further complicated by the production and shedding of fine roots, which can be substantial in some forests [*Vogt et al.*, 1986]; this litter is shed directly into the soil pool, blurring the distinction between litter production, litter pool, and SOM.

Litter production refers to plant material shed in 1 year; it is composed primarily of material such as leaves, fine wood, and fine roots shed in the same year they are produced. Some measurement reports describe litter composition. However, while

Table 1a. Summary of Data-Based and Model-Based Estimates of Litter Pools

Category / Reference, model	Parameter	Technique	Dry Matter, Pg	Carbon, Pg	Comments
		Litter Pool: Data			
Direct, implemented					
this study	litter pool	measurement compilation	136	68	leaf and other litter pool, forest/woodland
			25 (leaf)	13 (leaf)	
			111 (other)	55 (other)	
this study	CWD	ratio of live to CWD biomass	151 *	75	after *Harmon and Hua* [1991] and *Harmon et al.* [1993]
Ajtay et al. [1979]	littermass	ecosystem composites	138	69	
Direct, reported					
Whittaker and Likens [1975]	littermass	ecosystem composites	100-110 *	50-55	
Ajtay et al. [1979]	littermass	ecosystem composites	180 *	90	
			120 * (other)	60 (other)	
			60 * (dead wood)	30 (dead wood)	
Bazilevich [1974]	littermass	ecosystem composites	194 *	97	
		Litter Pool: Models/Regressions			
Direct, implemented					
Esser [1982], Hamburg	litter pool	HBM: NPP, decomposition	392	196 *	equilibrium
			120 (herb)	60 * (herb)	
			271 (wood)	136 * (wood)	
Direct, reported					
Esser et al. [1982], Hamburg	litter pool	HBM: NPP, decomposition	381	191	author' conversion = 0.55
Goudriaan and Ketner [1984]	litter pool	carbon model	116 *	58	
Esser [1987], Hamburg	litter pool	NPP, Decomposition	304 *	152	1981 results of transient run
Esser and Lieth [1989], Hamburg	litter pool	terrestrial biosphere model	168	84 *	
Esser and Lieth [1993], HRBM	litter pool	terrestrial biosphere model	184 *	92	1981 results of transient run
Rotmans and DenElzen [1993]	litter pool	terrestrial biosphere model	102 *	51	
Potter et al. [1993], CASA	litter pool	terrestrial biosphere model	348 *	174	leaf, fine root, and wood litter pools
			102 * (leaf)	51 (leaf)	
			86 * (fine root)	43 (fine root)	
			160 * (wood)	80 (wood)	
Esser and Lautens, [1994], OBM	litter pool	terrestrial biosphere model	222 *	111	preindustrial, equilibrium conditions
Esser [1996, pc], OBM	litter pool	terrestrial biosphere model	348 *	174	equilibrium conditions
*Esser [*1996, pc], OBM	litter pool	terrestrial biosphere model	166 *	83	transient results
Foley [1994], DEMETER	litter pool	terrestrial biosphere model	300 *	150	
Friedlingstein et al. [1994], SLAVE	litter pool	terrestrial biosphere model	132 *	64	
Hudson et al. [1994], GLOCO	litter pool	terrestrial biosphere model	94 *	47	

Implemented indicates that global distributions were developed by implementing models or extrapolating measurement or composite data. See text for explanation.

Dry matter is 0.5 carbon. Values are totals except as indicated in parentheses.

* Conversions from this study. Values without asterisks are those reported by authors.

distinctions between leaf litter and total litter are most often made, it is frequently unclear what component of woody material is included in the total. For instance, little or no information is provided about size thresholds for woody litter included in measurements. Roots may be included in some reports of litter pool (dead roots) or production (fine roots), but such distinctions are usually difficult to determine. For the most part, measurements exclude large dead wood, coarse woody roots, and production of fine roots. Thus, litter measurements essentially reflect aboveground litter production.

We use *Raich and Schlesinger's* [1992] definition of soil respiration (SR) as the sum of root respiration (RR, maintenance respiration of root biomass), surface litter respiration (decomposition of aboveground litterfall), and SOM respiration (decomposition of soil organic matter).

2.2. Approach and Rationale

The two indirect approaches used in this study to estimate litter production are based on soil respiration and on net primary production (NPP). The rationale for both assumes steady state in which net carbon exchange between atmosphere and biosphere is zero over the course of a year. In terms of processes, annual net carbon uptake by plants (NPP) is balanced by carbon return to the atmosphere through decomposition of SOM and litter. The latter two, combined with root respiration, comprise total soil respiration. Since SR is dominated by decomposition of fresh litter supplied via the current year's NPP, total litter production and NPP must be approximately equal. After subtraction of RR from SR, the balance also approximates total litter production. It's a simple procedure where litter is estimated from its major input (NPP) and from its major output (SR). Although it is unrealistic to assume that all ecosystems are in steady state, the indirect or proxy approaches allow evaluation of large-scale features and patterns if estimated fluxes and pools are substantially larger than ecosystems' carbon imbalances.

Table 1 is an overview of current litter production and pool estimates and the techniques by which they have been estimated. Table 2 distills the cases implemented in this study.

Table 1 distinguishes estimates implemented in this study (Table 2) from those reported by others. The latter are generally from more complex ecosystem models that could not be implemented here but represent state of the art. Because litter definitions vary among studies, Table 1 provides parameter names used by original authors as a guide to interpretation. Finally, because conversions between carbon and organic or dry matter vary among authors and among plant materials, estimates are provided in units of petagrams dry matter and petagrams carbon. Unless otherwise noted, the conversion factor used throughout assumes dry matter is 0.50 carbon, although assumptions of carbon content of organic matter in plants and soil can vary from 0.42 to 0.58 [*Ajtay et al.*, 1979].

Both litter pools (Table 1a) and litter production (Table 1b) are represented in the present study by data-based estimates (from measurements or ecosystem composites) (1D-4D in Table 2 and throughout) and by regression models (5M-10M in Table 2 and throughout). Each of these categories can include direct and indirect approaches although indirect approaches were available only for estimating litter production.

2.3. Data

Data-based techniques for estimating litter production and pools involve associating reported measurements, or values

Table 1b. Summary of Data-Based and Model-Based Estimates of Litter Production

Category Reference, model	Parameter	Technique	Dry Matter Pg	Carbon Pg	Comments
		Litter Production: Data			
Direct, implemented					
this study	litterfall	measurement compilation	39	20	above-ground, forest/wood/wooded grass
			26 (leaf)	13 (leaf)	
			13 (other)	7 (other)	
this study	coarse wood input	live biomass, mortality, and catastrophic inputs	12 *	6	
Ajtay et al. [1979]	litterfall	ecosystem composites	107	54 *	
Direct, reported					
Reiners [1973]	litter input	ecosystem composites	92	46 *	
			128	64 *	
			125	62 *	
			75	37 *	
Ajtay et al. [1979]	litterfall	ecosystem composites	95	43	author's conversion = 0.45
Indirect, implemented					
this study	litter production	SR - RR: ecosystem composites	93 *	47	
Indirect, reported					
Fung et al. [1987]	NPP	ecosystem composites, latitude	89 *	45	
Ajtay et al. [1979]	NPP	ecosystem composites	133	60	author's conversion = 0.45
Whittaker and Likens [1975]	NPP	ecosystem composites	97 *	48	

Table 1b. continued

Category Reference, model	Parameter	Technique	Dry Matter Pg	Carbon Pg	Comments
		Litter Production: Models/Regressions			
Direct, implemented					
Meentemeyer et al. [1982]	litter production	regression: AET	54	27 *	leaf and total litterfall
			34 (leaf)	17 * (leaf)	
			20 (other)	10 * (other)	
Lonsdale [1988]	litterfall	regression: latitude altitude	29	15	leaf and total litterfall, forest/woodland
			21 (leaf)	11 * (leaf)	
			8 (other)	4 * (other)	
Direct, reported					
Goudriaan and Ketner [1984]	litterfall	biosphere model	85 *	43	
Rotmans and DenElzen [1993]	litterfall	biosphere model	95 *	48	leaf and total litterfall
			46 * (leaf)	23 (leaf)	
			49 * (other)	25 (other)	
Indirect, implemented					
this study	litter production	SR - RR: climate	100	50	total above-ground litter production
Rosenzweig [1968]	NPP	regression: AET	139	70 *	above-ground NPP
Lieth [1975], Miami model	NPP	regression: T, P	131	66 *	
Esser [1982], Hamburg model	NPP	regression: T, P, soil fertility	118	59 *	herbaceous, wood and total NPP
			56 (leaf)	28 * (leaf)	
			62 (wood)	31 * (wood)	
Indirect, reported					
Lieth [1975], Miami	NPP	regression: T, P	106 *	53	
Esser et al. [1982], Hamburg	NPP	regression: T, P, soil fertility	118	59 *	herbaceous, wood and total NPP
Goudriaan and Ketner [1984]	NPP	carbon model	134 *	62	
Esser [1987], Hamburg	NPP	terrestrial biosphere model	97 *	49	1981 results from transient run
Box et al. [1988]	NPP	terrestrial biosphere model	135 *	68	
Dai and Fung [1993], ~ Miami	NPP	regression: T, P	108 *	54	
Melillo et al. [1993], TEM	NPP	terrestrial biosphere model	102 *	51	
Potter et al. [1993], CASA	NPP	terrestrial biosphere model	96 *	48	
Rotmans and DenElzen [1993]	NPP	terrestrial biosphere model	121 *	60	
Foley [1994], DEMETER	NPP	terrestrial biosphere model	124 *	62	
Hudson et al. [1994], GLOCO	NPP	terrestrial biosphere model	95 *	47	
Ruimy et al. [1994]	NPP	NPP model	118 *	59	
Warnant et al. [1994], CARAIB	NPP	terrestrial biosphere model	129 *	65	
Bonan [1995]	NPP	GCM and biosphere model	84	42 *	

Implemented indicates that global distributions were developed by implementing models or extrapolating measurement or composite data. See text for explanation.
Dry matter is 0.5 carbon. Values are totals except as indicated in parentheses.
* Conversions from this study. Values without asterisks are those reported by authors.

Table 2. Outline of Cases Implemented in This Study

Case/Reference		Parameter	Technique	Total Pg dm*
1D	This study	above-ground litter production	measurements	39
		litter pool	measurements	136
2D	*Ajtay et al.* [1979]	litterfall	composites	107
		litter mass	composites	138
3D	This study	litter production (SR-RR)		93
		SR (144): composites		
		RR (51): composites		
4D	This study	CWD production	composites and model	12
		CWD pool	composites and model	151
5M	This study	litter production (SR-RR)		100
		SR (160): regression with T, P		
		RR (60): composites		
6M	*Meentemeyer et al.* [1982]	litter production	regression: AET	54
7M	*Lonsdale* [1988]	forest litter production	regression: latitude, altitude	29
8M	*Rosenzweig* [1968]	above-ground NPP	regression: AET	139
9M	*Lieth* [1975]	total NPP	regression: T, P	131
10M	*Esser et al.* [1982]	total NPP	regression: T, P, soil fertility	118
		litter pool	NPP and decomposition	392

* Litter pool reported in Pg dm; litter production/litterfall reported in Pg dm/yr.

composited from such measurements, with vegetation types in the data base of Matthews [1983]; these values are then extrapolated globally using the 1° latitude by 1° longitude digital data. For the modeled cases (5M-10M) the vegetation data set is used to sort locations by vegetation type and ecosystem means, computed over the distribution of each type, are reported. This facilitates comparisons among distributions whether or not they are derived from the vegetation data.

2.3.1. Vegetation. The vegetation data base [*Matthews*, 1983] was compiled from about 70 published maps using the hierarchical UNESCO vegetation-classification system [*Unesco*, 1973]. Globally, 178 vegetation types are distinguished in the data base; for this study we relied on a widely used version that distinguishes 29 types of vegetation and a desert (bare soil) category. Plate 1 shows the distribution of vegetation types aggregated to 12 types and ice. Global areas and brief descriptions of the vegetation types, along with their map associations, are presented in Table 3. Areas reflect preagricultural conditions for the present climate; cultivated lands were not included in order to maintain compatibility with climate-based estimates which consider only natural vegetation.

2.3.2. Topography. One model implemented in this study [*Lonsdale*, 1988] relies on latitude and elevation to estimate litter production of forests. We used a modified version of the 1° resolution Rand topography data set published by *Gates and Nelson* [1974]. The data set identifies 1° cells as land, lake or ocean; heights and depths of land and water, respectively, are also provided. For consistency, the criterion for including land cells in the vegetation and topography data sets is that they are composed of ≥50% land. Land and water fractions of cells were determined from a global series of Operational Navigation Charts (ONCs) published at 1:1 million scale by the Defense Mapping Agency. Land/water designations were inconsistent for ~1500 1° cells between the Rand and ONC data sets. About half these cells retained the Rand designations because they were very close to the 50% threshold. The balance were reclassified, and elevations or water depths were appended as appropriate. Land totals 14,628 cells excluding permanent ice locations. Configurations of all data bases used in this study are consistent with the land-water distributions of the revised topography data set.

2.3.3. Climate and water balance. Several models in this study require temperature and precipitation data as well as parameters derived from them such as potential evapotranspiration (PET) and actual evapotranspiration (AET) (Table 1). Calculating AET further requires global data on soil texture and water-holding capacity of soils; we used those described by *Bouwman et al.* [1993] based on the soil data of *Zobler* [1986].

2.3.3.1. Temperature and precipitation: Several gridded climatologies of temperature and precipitation originate from similar long-term records from weather stations [e.g., *Shea,* 1986; *Legates and Willmott,* 1990; *Leemans and Cramer*, 1991]. Variations among them are due to differences in threshold record lengths for individual stations and in interpolation techniques, corrections for effects of elevation and urban areas, and other factors. Throughout this study we used *Shea's* [1986] monthly and annual climatology for temperature and precipitation to maintain consistency with soil hydrology data sets [*Bouwman et al.*, 1993].

2.3.3.2. Actual and potential evapotranspiration: Potential evapotranspiration is the maximum amount of water that can evaporate from a surface with an unlimited water supply. AET, which is ≤PET, is the actual amount of water evaporated from the surface, and D (deficit) is PET - AET. The water balance model described by *Bouwman et al.* [1993] was

Table 3. Vegetation Types and Their Preagricultural Areas as Used in This Study

Vegetation Type		Area 10^{12} m^2	Description
1	(1)	12.8	tropical evergreen rainforest, mangrove
2	(2)	4.1	tropical/subtropical evergreen seasonal broadleaved forest
3	(2)	0.2	subtropical evergreen rainforest
4	(1)	0.4	temperate/subpolar evergreen rainforest
5	(2)	1.2	temperate evergreen seasonal broadleaved forest, summer rain
6	(2)	0.6	evergreen broadleaved sclerophyllous forest, winter rain
7	(2)	0.5	tropical/subtropical evergreen needleleaved forest
8	(2)	9.5	temperate/subpolar evergreen needleleaved forest
9	(3)	4.0	tropical/subtropical drought-deciduous forest
10	(3)	7.7	cold-deciduous forest, with evergreens
11	(3)	5.5	cold-deciduous forest, without evergreens
12	(10)	3.1	xeromorphic forest/woodland
13	(4)	2.3	evergreen broadleaved sclerophyllous woodland
14	(4)	2.6	evergreen needleleaved woodland
15	(5)	4.7	tropical/subtropical drought-deciduous woodland
16	(5)	2.6	cold-deciduous woodland
17	(6)	1.6	evergreen broadleaved shrubland/thicket and dwarf shrubland
18	(6)	0.7	evergreen needleleaved or microphyllous shrubland/thicket
19	(7)	1.0	drought-deciduous shrubland/thicket and dwarf shrubland/thicket
20	(7)	0.5	cold-deciduous subalpine/subpolar shrubland and dwarf shrubland
21	(10)	9.4	xeromorphic shrubland/dwarf shrubland
22	(11)	7.2	arctic/alpine tundra/mossy bog
23	(8)	8.5	tall/medium/short grassland with 10-40% tree cover
24	(8)	4.2	tall/medium/short grassland with <10% tree or tuft-plant cover
25	(8)	10.7	tall/medium/short grassland with shrub cover
26	(9)	1.5	tall grassland, no woody cover
27	(9)	1.5	medium grassland, no woody cover
28	(9)	7.3	meadow/short grassland, no woody cover
29	(9)	0.3	forb formations
30	(12)	15.8	desert (bare soil)
Total		132.0	

Data are from *Matthews* [1983]. Numbers in parentheses indicate associations with general types mapped in Plate 1.

used here to calculate PET, AET, and D on a monthly timescale summed to annual values. The model is adapted from that of *Mintz and Serafini* [1981] and estimates evaporation according to *Thornthwaite* [1948]. Large-scale patterns in these climate data are consistent with reported values [e.g., *Baumgartner and Reichel*, 1975; *Miller*, 1977; *Mintz and Walker*, 1993].

The proportionality between PET and P, which indicates the relationship between local evaporative demand and precipitation, is >1 for water-limited ecosystems such as shrublands, grasslands, tundra, and drought-deciduous forest, and <1 for humid ecosystems. For example, PET/P is 3.2 for xeromorphic shrubland and 2.6 for shrub grassland; for humid forests, PET/P ranges from 0.5 (temperate rainforest) to 0.9 (temperate cold-deciduous forest).

The proportionality between AET and PET, indicating how efficiently the vegetation/soil/atmosphere system supplies local evaporative demand, is a function of precipitation, soil water-holding capacity, vegetation, and soil texture, and ranges from ≤0.55 for most arid woodlands, arid shrublands, and grasslands, to >0.9 for tropical, subtropical, and temperate rainforests as well as temperate and tropical seasonal evergreen forests. These evaporation parameters for ecosystems agree reasonably well with those reported by, e.g., *Galoux et al.* in *Reichle* [1981] and *Vogt et al.* [1986]. For example, for mediterranean forest (type 6) AET is 445 mm/yr and 475 mm/yr from *Galoux et al.* [1981] and this study, respectively. For boreal coniferous forest, *Galoux et al.* [1981] report 631 mm/yr mean precipitation and AET averaging 357-430 mm/yr equal to 56-68% of P; forested boreal ecosystems in this study (types 8 and 14) exhibit mean precipitation values of 596 and 629 mm/yr, respectively, and AET of 395 and 392 mm/yr, respectively, equal to 66% and 62% of annual precipitation.

Table 4a. Data Compilations and Reported/Recorded Site Characteristics

Reference	Number of Sites	Veg.	Locale	Lat.	Lon.	Alt.	Temp.	Precip.	Age	Meas. Period	Parameters Recorded
Bray and Gorham [1964], Table 4	293	X	X	X	X	X	...	...	X	...	litterfall: leaf, other, total
Singh and Gupta [1977], Table 3	61	X	X	...	...	...	...	...	...	...	daily decomposition rates
Anderson and Swift [1984], Table 1	35	X	X	...	...	X	...	...	...	...	litterfall, standing crop, and turnover coefficients: leaf and total litter
Proctor [1984], Tables 1-6	218	X	X	X	...	X	X	X	...	X	litter: leaf, total
Vitousek [1984], Table 1	122	X	X	X	...	X		X	X	...	fine litterfall
Vogt et al. [1986], Appendix 1 (aboveground)	206	X	X	X	...	X	X*	X	...	...	forest floor: mass, MRT; litterfall: fine, wood
Vogt et al. [1986], Appendix 2 (belowground)	111	X	X	X	...	X	X*	X	...	...	forest floor mass and root mass: live, dead, total
Harmon et al. [1986], Table 1	32	X	X	...	...	...	...	...	...	X	coarse woody detritus: annual input
Harmon et al. [1986], Table 5	61	X	X	...	...	...	...	...	X	...	coarse woody detritus: biomass
Harmon et al. [1986], Table 7	15	X	X	...	...	...	...	...	...	...	CWD percent of dead/downed wood
Brown and Lugo [1982], Appendix 5	35	...	...	...	...	...	X	X	...	...	organic matter in litter
Brown and Lugo [1982], Appendix 3	73	...	...	...	...	...	X	X	...	...	litterfall: leaf/friut, total
Raich and Nadelhoffer [1989], Appendix	53	X	X	X	...	...	...	...	X	...	litterfall, soil respiration
Raich and Schlesinger [1992], Appendix	171	X	X	X	X	...	...	...	...	...	soil respiration

X indicates that mean annual temperature is reported for sites.
* Mean monthly maximum and mean monthly minimum temperatures are also reported.

Table 4b. Summary of Published Measurements of Litter Production and Pools, by Vegetation Type, Compiled for This Study

Veg. Type	Area $10^{12}m^2$	Production Total	Production Leaf	Production Leaf and Total	Pool
1	12.8	158	80	71	22
2	4.1	48	25	20	42
3	0.2	34	20	13	...
4	0.4	7	11	17	...
5	1.2	2	3	2	...
6	0.6	25	13	10	7
7	0.5	43	17	3	21
8	9.5	204	39	15	108
9	4.0	21	17	11	1
10	7.7	24	9	10	3
11	5.5	152	21	5	53
12	3.1	...	...	...	...
13	2.3	...	...	...	...
14	2.6	3	...	...	...
15	4.7	4	6	3	...
16	2.6	23	7	5	10
17	1.6	1	1	...	...
18	0.7	...	...	...	...
19	1.0	...	...	...	...
20	0.5	...	...	...	...
21	9.4	...	...	...	...
22	7.2	...	...	...	...
23	8.5	2	4	2	...
24	4.2	2	1	...	...
25	10.7	1	2	1	...
26	1.5	...	...	...	...
27	1.5	...	...	...	...
28	7.3	...	...	...	...
29	0.3	...	...	...	...
30	15.8	0 *	0 *	0 *	0 *
Sum	132.0	754	276	188	267

Duplicate reports for the same site are excluded. All pool values are from the compilation of *Vogt et al.* [1986]; areas are from *Matthews* [1983].
* In the *Matthews* [1983] data set, type 30 (desert/bare soil) is defined by the absence of vegetation and therefore is considered measured with zero measurements.

2.3.4. Litter measurements. We integrated compilations of measurements on litter production, pools, decomposition rates, and turnover times, relying heavily on the following: *Bray and Gorham* [1964] who report 293 measurements of litter production for a variety of ecosystems; *Singh and Gupta* [1977] with decomposition rates for 61 sites; *Anderson and Swift* [1983] with litterfall measurements for 35 tropical sites; *Proctor* [1984] who gives litterfall measurements for 218 tropical forest sites; *Vitousek* [1984] with litterfall measurements for 122 tropical sites; *Harmon et al.* [1986] reporting input, biomass, and dynamics of coarse woody detritus (CWD) for 108 forests; *Vogt et al.'s* [1986] analysis of measurements for aboveground litter production and pools (206 forest sites) and belowground detrital production (111 forest sites); *Brown and Lugo* [1982] who report litter production measurements in 73 tropical and subtropical forest sites, and organic matter in litter pools for 35 tropical and subtropical forest sites; *Raich and Nadelhoffer* [1989] with litterfall and soil respiration measurements for 53 sites; and *Raich and Schlesinger* [1992] reporting soil respiration measurements for 171 sites throughout all major ecosystems. Many other measurements have been published individually in addition to these compilations but examination of this large body of literature was beyond the scope of this project.

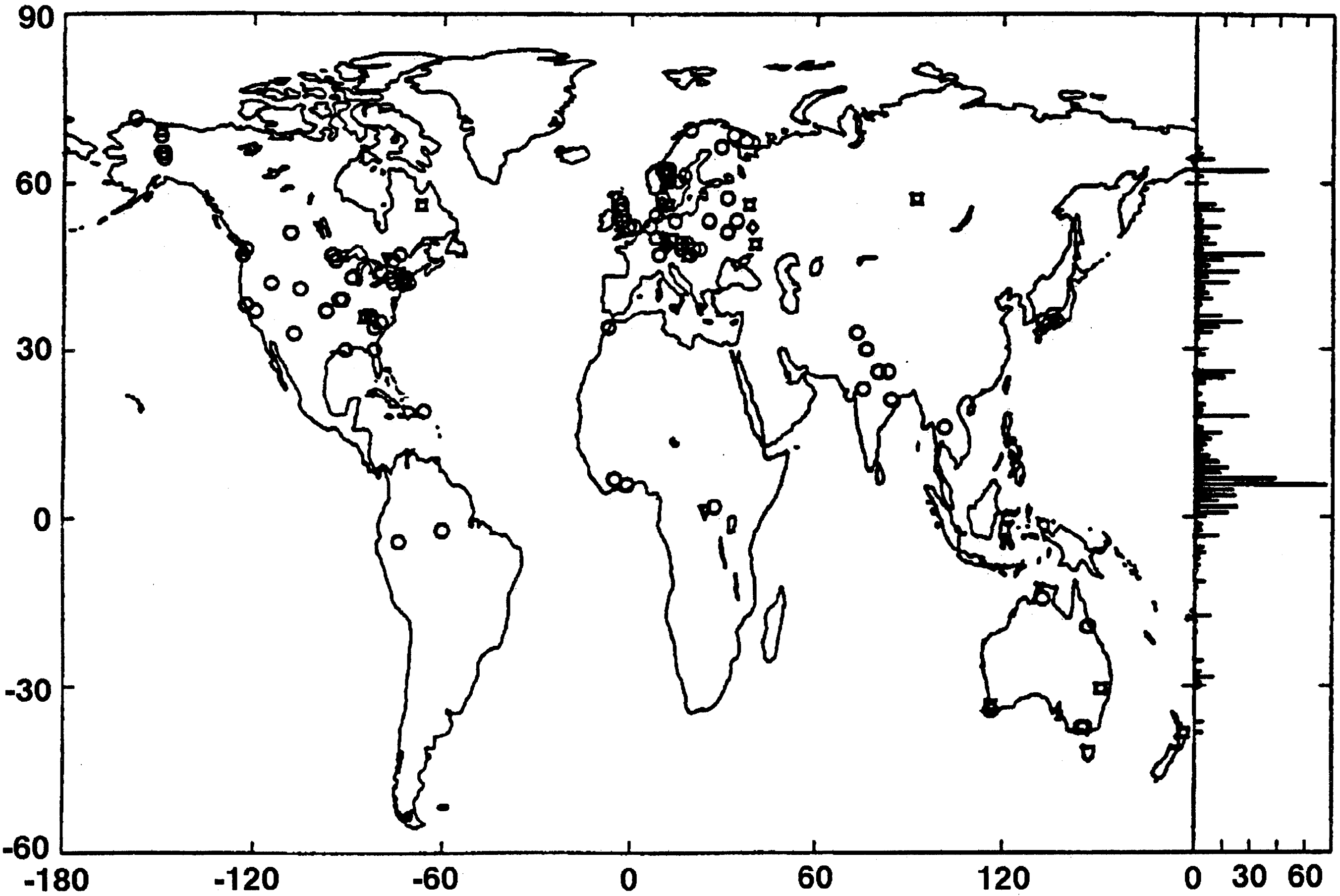

Figure 1. Location map of ~1100 measurements. Symbols show numbers of measurements in 1° cells. Sites with sufficient identifying information (30%) are shown at their reported locations. The latitudinal distribution of measurements for which insufficient location information is provided (70%) is shown in the right-hand plot. Symbols: circle, 1-4 measurements, square, 5-8 measurements, triangle, 9-12 measurements, diamond, 13-16 measurements, and star, ≥17 measurements.

Table 4a summarizes the compilations and site features used in this study. Information on the characteristics listed in the table was always recorded if provided in the compilation sources. However, the sources frequently report additional parameters and measurements, such as nutrient content of litter constituents, that are not included here. Several procedures were carried out to integrate, compare, and cross-reference the measurements from these compilations. For example, common species names were appended to Latin names and Latin names to common names throughout; available location information was standardized and entered via a hierarchy indicating country, region, and local place name; sites were given alphanumeric codes identifying them within individual compilations, as well as numeric codes uniquely identifying them within the fully integrated data set. In this way, information on original and compilation sources is preserved for each site.

Because compilations vary with respect to identifying and ancillary information provided with the measurements, duplicate reports of a single site were not necessarily easy to identify. References for the sites are always provided and often allow identification of duplicate reports among compilations. However, difficulties arise in cases in which early compilers [e.g., *Bray and Gorham*, 1964] report measurements via private communications that are later published; later compilers then refer to the published works. Furthermore, some compilers report original authors for measurements while others report authors of an intermediate compilation, such as *DeAngelis et al.* [1981]. Another difficulty in identifying duplicate reports is that compilers may obtain information on site characteristics such as elevation, temperature and precipitation from other descriptions of the sites, from maps and meteorological stations, or from gridded data bases. Sometimes these cases are identified [e.g., *Vitousek* , 1984] but often no mention of the alternative sources is made. The result is identical measurements with different site characteristics or identical sites with different measurement results. In the case of Brown and Lugo [1982], translation of the original vegetation descriptions into *Holdridge's* [1947] lifezone nomenclature, along with minimal site information, makes cross-referencing especially difficult. Differences in reporting units and conversion units (dry matter, carbon, CO_2) among authors and compilers means that repeated conversions and rounding obscure both similarities and differences in the measurements. Finally, because of the large volume of data, typographical and other errors in the source compilations were unavoidable. Table 4a shows that a basic characteristic such as longitude, which can be crucial to unequivocal site identification, is frequently missing from the compilation sources; longitude is

Table 5. Litter Production by Vegetation Type

		Data-Based Estimates				Model-Based Estimates					
Vegetation Type	Area 10^{12} m^2	1D This Study Measurem.	2D Ajtay Composites	3D This Study SR-RR	4D This Study CWD	5M This Study SR-RR	6M Meentem. AET	7M Lonsdale Lat., Alt.	8M Rosenzweig AET	9M Lieth T, P	10M Esser T, P, Soil
1	12.8	910	1850	1512	360	1449	1180	879	3544	2208	1698
2	4.1	719	1300	1512	360	1172	904	621	2444	1895	1576
3	0.2	716	1850	1512	360	876	660	428	1614	1566	1467
4	0.4	549	550	386	420	681	421	298	900	1401	1187
5	1.2	565	850	776	200	923	721	457	1762	1765	1431
6	0.6	532	1000	856	140	680	296	361	638	1043	1106
7	0.5	481	1300	960	260	814	545	382	1247	1611	1234
8	9.5	299	600	1204	200	383	214	226	456	708	555
9	4.0	447	1300	808	20	1114	827	613	2162	1738	1746
10	7.7	448	850	776	180	574	389	310	871	1108	980
11	5.5	399	850	776	180	422	285	261	618	809	739
12	3.1	...	125	291	20	1063	715	...	1836	1434	1538
13	2.3	...	1000	291	20	894	446	496	1046	1125	1037
14	2.6	608	600	563	120	462	214	692	489	657	610
15	4.7	385	1300	875	180	1053	546	691	1293	1435	1477
16	2.6	258	1300	419	100	199	86	175	224	240	168
17	1.6	140	125	451	40	780	168	...	408	615	589
18	0.7	...	300	451	40	502	139	...	331	549	502
19	1.0	...	125	314	20	864	354	...	885	851	857
20	0.5	...	200	451	20	326	129	...	304	468	382
21	9.4	...	125	314	...	724	148	...	339	550	481
22	7.2	...	300	96	...	296	90	...	223	315	240
23	8.5	290	800	944	...	1108	566	...	1420	1328	1296
24	4.2	160	1500	944	...	1214	628	...	1571	1385	1375
25	10.7	320	1500	663	...	856	253	...	594	747	784
26	1.5	...	900	707	...	1122	578	...	1362	1344	1350
27	1.5	...	550	707	...	926	387	...	883	975	1125
28	7.3	...	550	707	...	737	212	...	478	763	705
29	0.3	...	550	96	...	473	154	...	339	580	360
30	15.8	0	0	0	...	253	48	...	107	242	188
Total area	132	97	132	132	66	132	132	59	132	132	132
Total prod.		39	107	93	12	100	54	29	139	132	118
Mean prod.		401	811	705	183	758	409	493	1054	1000	894

Production, except for totals, is g $dm/m^2/yr$.

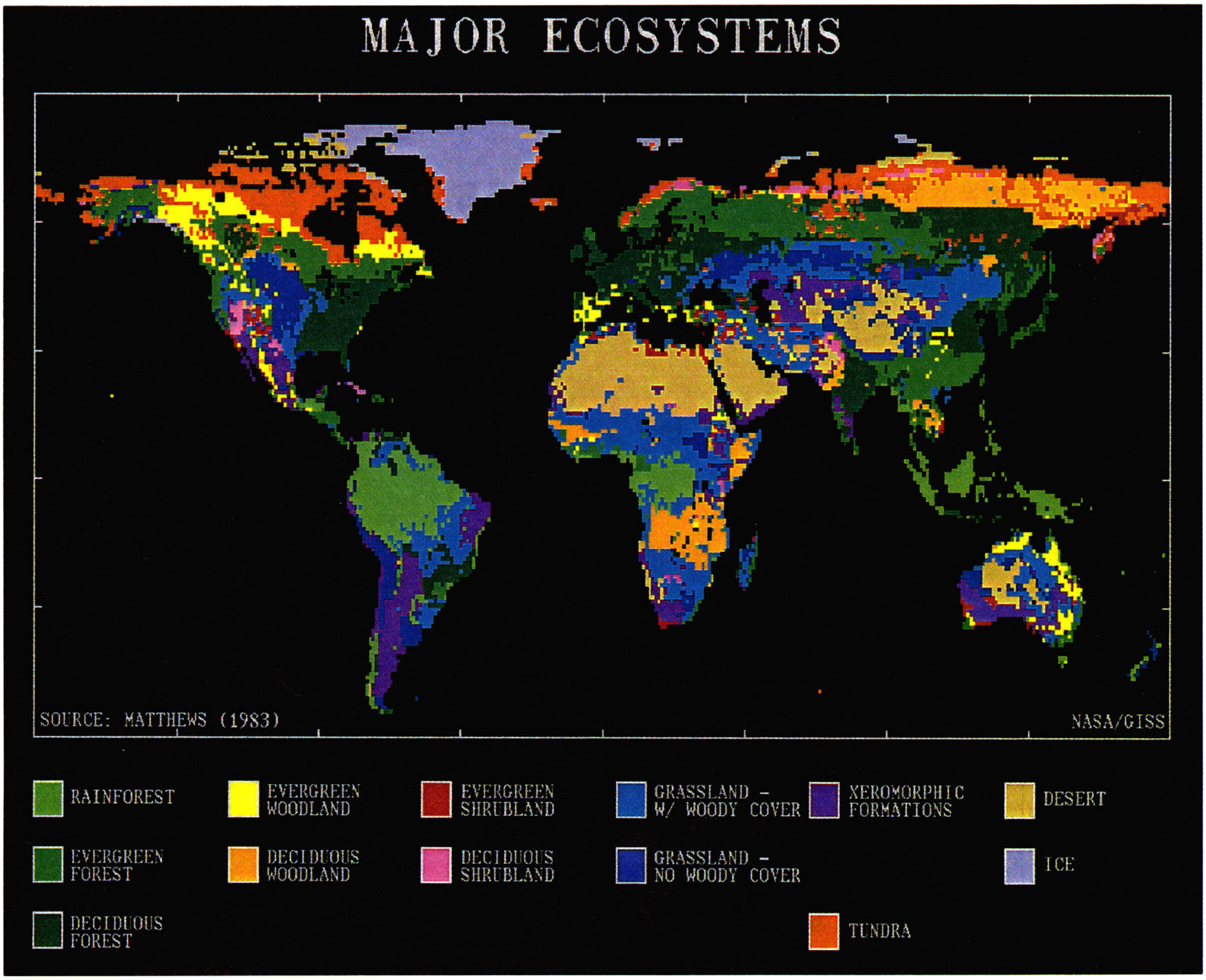

Plate 1. Vegetation map from the data of *Matthews* [1983]. Vegetation types from Table 3 are clustered into the following twelve groups: 1, rainforest, 2, evergreen forest, 3, deciduous forest, 4, evergreen woodland, 5, deciduous woodland, 6, evergreen shrubland, 7, deciduous woodland, 8, grassland with woody cover, 9, grassland with no woody cover, 10, xeromorphic formations, 11, tundra, and 12, desert/bare soil.

reported for only ~30% of all measurements compiled for this study, which is somewhat lower than the reporting frequency in primary documents [E. Holland, private communication, 1996].

Integration of the compilations produced a total of 1317 sites including many duplications. Of that total, 39 mangrove sites were set aside because of their unique characteristics, 149 mainly agricultural sites were removed, and 15 sites remain unclassified. Of the remaining 1114 sites, 754 report total fine litter production, 276 report leaf litter production, 188 report both, and 272 are duplicate measurements. Litter pool is reported for 267 sites. Tropical rainforest (type 1) and boreal needleleaved forest (type 8) are well represented. In fact, they are over-represented, relative to their areal coverage. Forests (types 1-11) and woodlands (13-16) are covered to varying degrees; shrublands, grasslands, and xeromorphic formations are very sparsely represented in the production measurements.

Figure 1 shows the geographic distribution of the measurements for the sites accompanied by information sufficient to locate them; symbols indicate the number of measurements per 1° cell. The graph on the right represents the latitudinal distribution of the ~70% of the measurement sites whose geographic locations are identified only by latitude.

Table 4b provides a summary of ecosystem coverage of the final data set used in this study along with area statistics for ecosystems. Substantial ecosystem gaps exist in the data set, although ecosystems with larger litter production, such as forests, are reasonably well represented. Close to 85% of the production measurements occur in six ecosystems that occupy ~21% of the ice-free land terrestrial surface: temperate/subpolar evergreen needleleaved forests (type 8) (27% of production measurements), tropical evergreen forests (type 1) (21%), and cold-deciduous forest without evergreens (type 11) (20%); each of several tropical and subtropical evergreen forests (types 2, 3, and 7) is represented by ~5% of the measurement

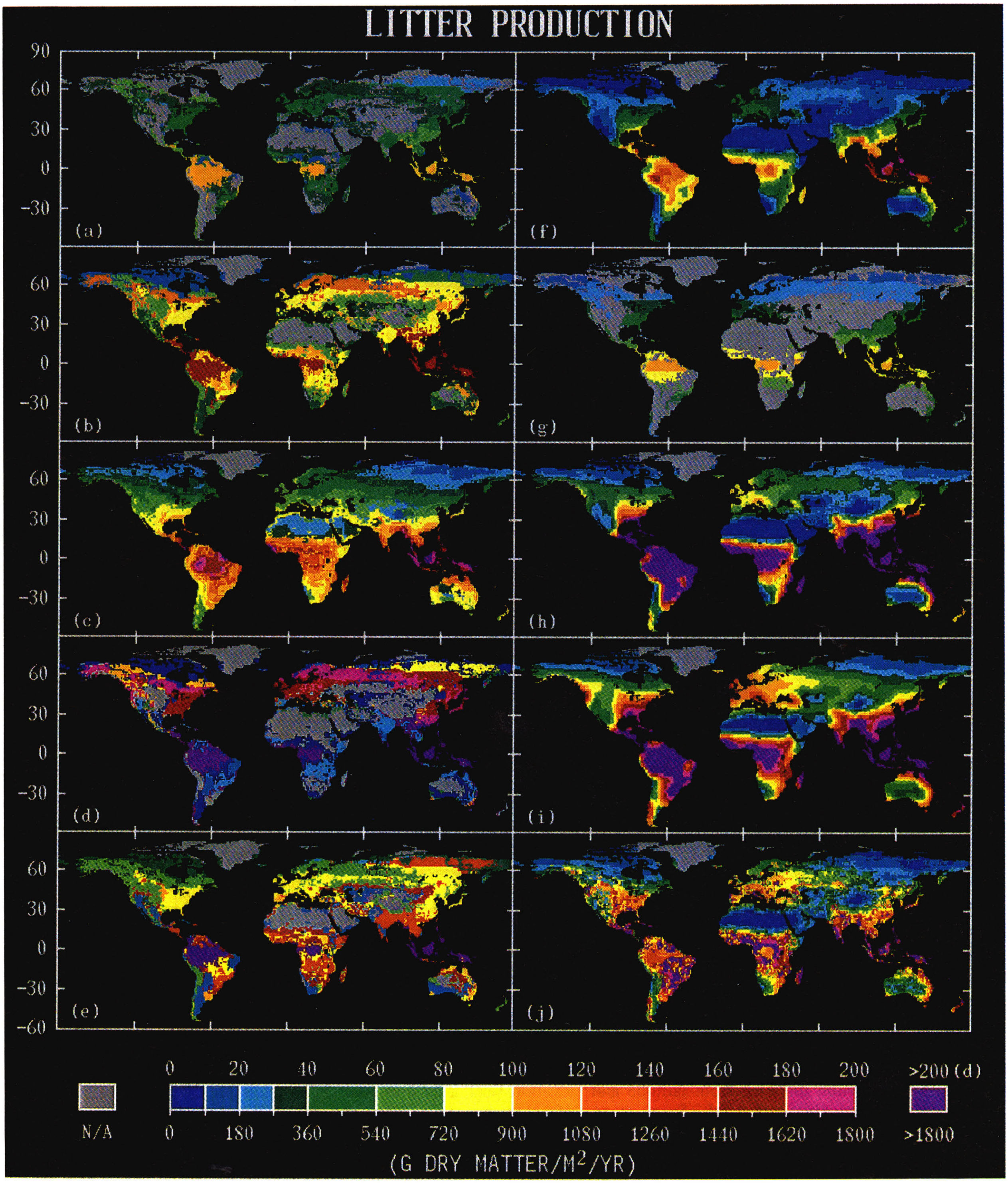

Plate 2. Geographic distributions of litter production. Refer to Table 2 for description of cases: (a) 1D, this study, aboveground litter production from measurement compilation; (b) 3D, this study, litter production, soil respiration ecosystem composites of *Raich and Schlesinger* [1992] minus ecosystem estimates of root respiration; (c) 5M, this study, soil respiration modeled from climate [*Raich and Schlesinger*, 1992] minus ecosystem estimates of root respiration; (d) 4D, this study, coarse woody detritus based on *Harmon and Hua* [1991]; (e) 2D, ecosystem litterfall composites of *Ajtay et al.* [1979]; (f) 6M, litter production modeled from actual evapotranspiration (AET) [*Meentemeyer et al.*, 1982]; (g) 7M, forest litter production modeled from latitude and elevation [*Lonsdale,* 1988]; (h) 8M, aboveground net primary productivity modeled from AET [*Rosenzweig*, 1968]; (i) 9M, total net primary productivity modeled from temperature and precipitation (Miami model of *Lieth* [1975]); (j) 10M, total net primary productivity modeled from temperature, precipitation, and soil factors (Hamburg model of *Esser et al.* [1982]).

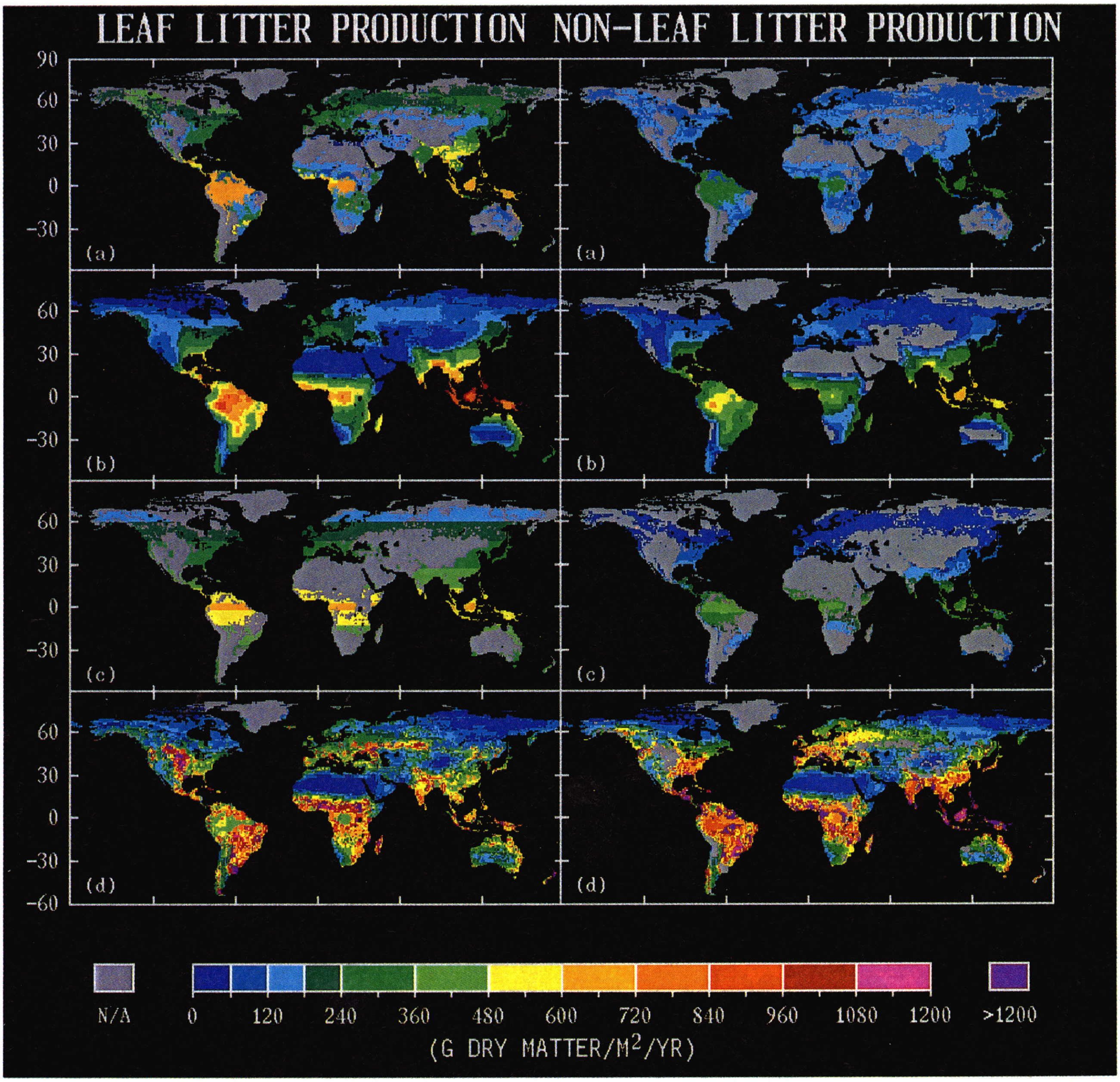

Plate 3. Geographic distribution of litter production components: (a) 1M, this study, aboveground litter production from measurement compilation (leaf and other litter totals are 26 and 13 Pg, respectively); (b) 6M, *Meentemeyer et al.* [1982], litter production modeled from AET (leaf litter and other litter totals are 34 and 20 Pg, respectively); (c) 7M, *Lonsdale* [1988], forest litter production modeled from latitude and elevation (leaf litter and other litter totals are 29 and 8 Pg, respectively); (d) 10M, *Esser et al.* [1982], herbaceous litter and wood litter modeled from temperature, precipitation, and soil factors (herbaceous and other litter total 56 and 62 Pg, respectively).

suite. Wooded grasslands (types 23-25) are poorly represented in production measurements and not represented at all for litter pools, while non-wooded grasslands (types 26-29), some shrublands (types 19-20), and xeromorphic formations (types 12 and 21) are not yet represented at all in this compilation.

The 267 measurements of forest litter pools are exclusively from the analysis of *Vogt et al.* [1986] (Table 4b). About 40% of the measurements are from temperate/boreal evergreen needleleaved forests (type 8); 4% are from boreal cold-deciduous woodlands (type 16); 21% are from temperate deciduous forests (types 10-11), 8% are from tropical rainforests (type 1), ~16% are from other tropical/subtropical seasonal broadleaved forests (type 2), and 8% from tropical/subtropical needleleaved evergreen forests (type 7). Although this series represents ecosystems that occupy only ~50% of the Earth's ice-free land surface, wooded ecosystems with larger litter pools are well represented.

3. Litter Production

We present 10 global distributions of litter production (Table 2). Nine are for fine litter and one is for CWD; four,

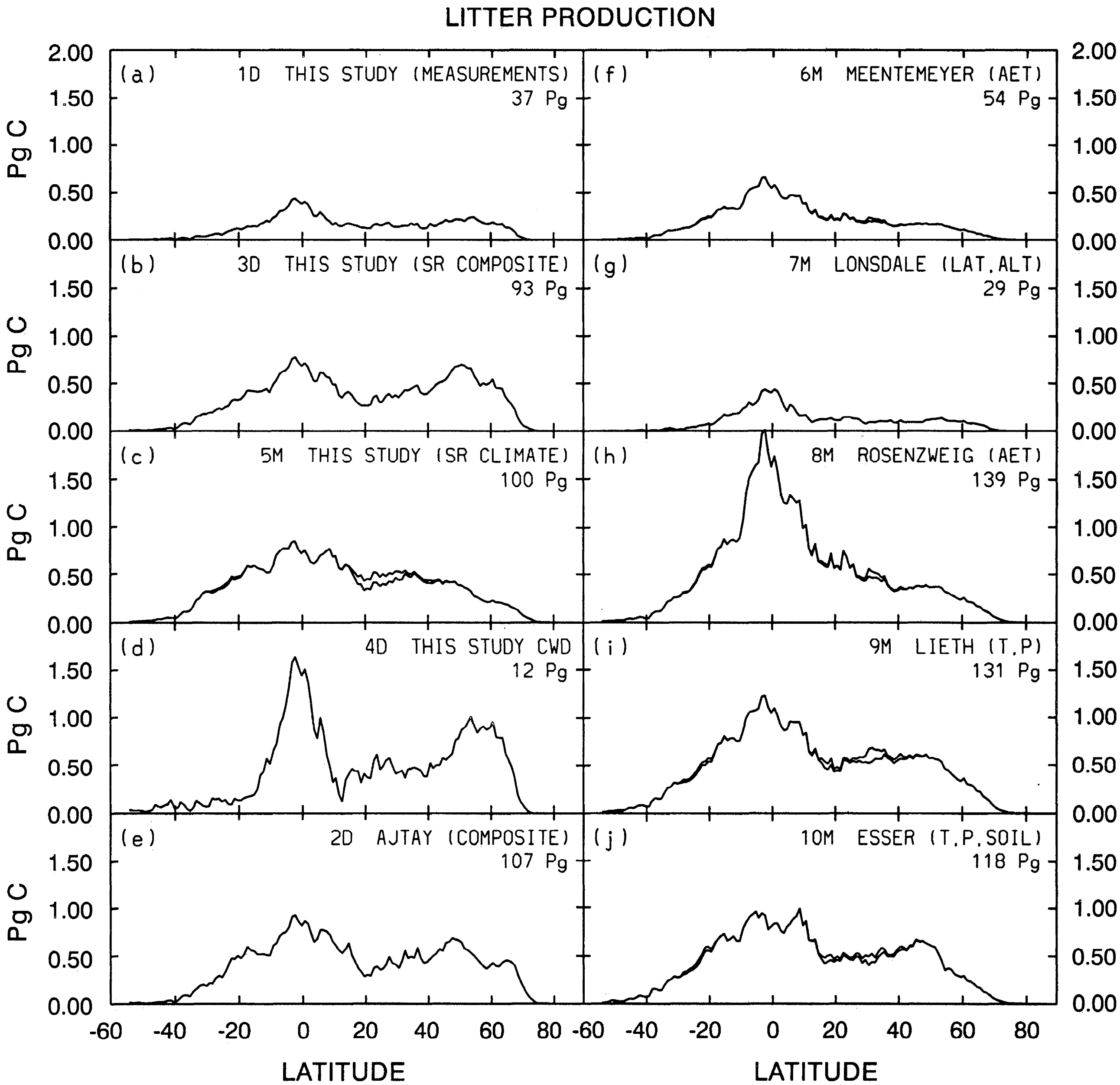

Figure 2. Same as Plate 2 except parameter is 1° total zonal litter production. Light lines are values using models directly; heavy lines are the same except deserts are set to zero.

including the distribution for CWD, are data based (1D-4D) and six are model-based (5M-10M). Production estimates discussed in this section are presented in tabular form, by ecosystem (Tables 2 and 5), as latitude/longitude distributions (Plate 2), and as zonal totals (Figures 2, 3, and 4).

3.1. Data-Based Production Estimates

3.1.1. Direct approaches. Litter production was estimated from the measurement compilation and from published ecosystem composites [*Ajtay et al.*, 1979] (1D and 2D, respectively, in Table 2). Ecosystem means for aboveground litter production were derived from the measurements and extrapolated using the vegetation data of *Matthews* [1983]. The ecosystem composites of *Ajtay et al.* [1979] were also matched with data of *Matthews* [1983] for extrapolation. Aboveground litter production rates from the compilation and from the Ajtay composites are listed by ecosystem in Table 5 and shown in Plates 2a and 2e, respectively; latitudinal sums are shown in Figures 2a and 2e, respectively.

Litter production from the compilation, 39 Pg dm/yr, averages ~400 g dm/m^2/yr for the wooded ecosystems represented in the data set. This is a partial estimate for the following reasons. First, there are currently no measurements to represent 12 ecosystems totaling ~25% of the ice-free land surface of the globe (Table 4b). Secondly, the estimate accounts only for aboveground production. For reasons discussed below, including these ecosystems may add 5-15 Pg dm while including underground production may double that estimate to 88-108 Pg dm/yr.

Using the Ajtay composites, we calculate total production to be 107 Pg dm/yr (Table 5). The zonal distribution (Figure

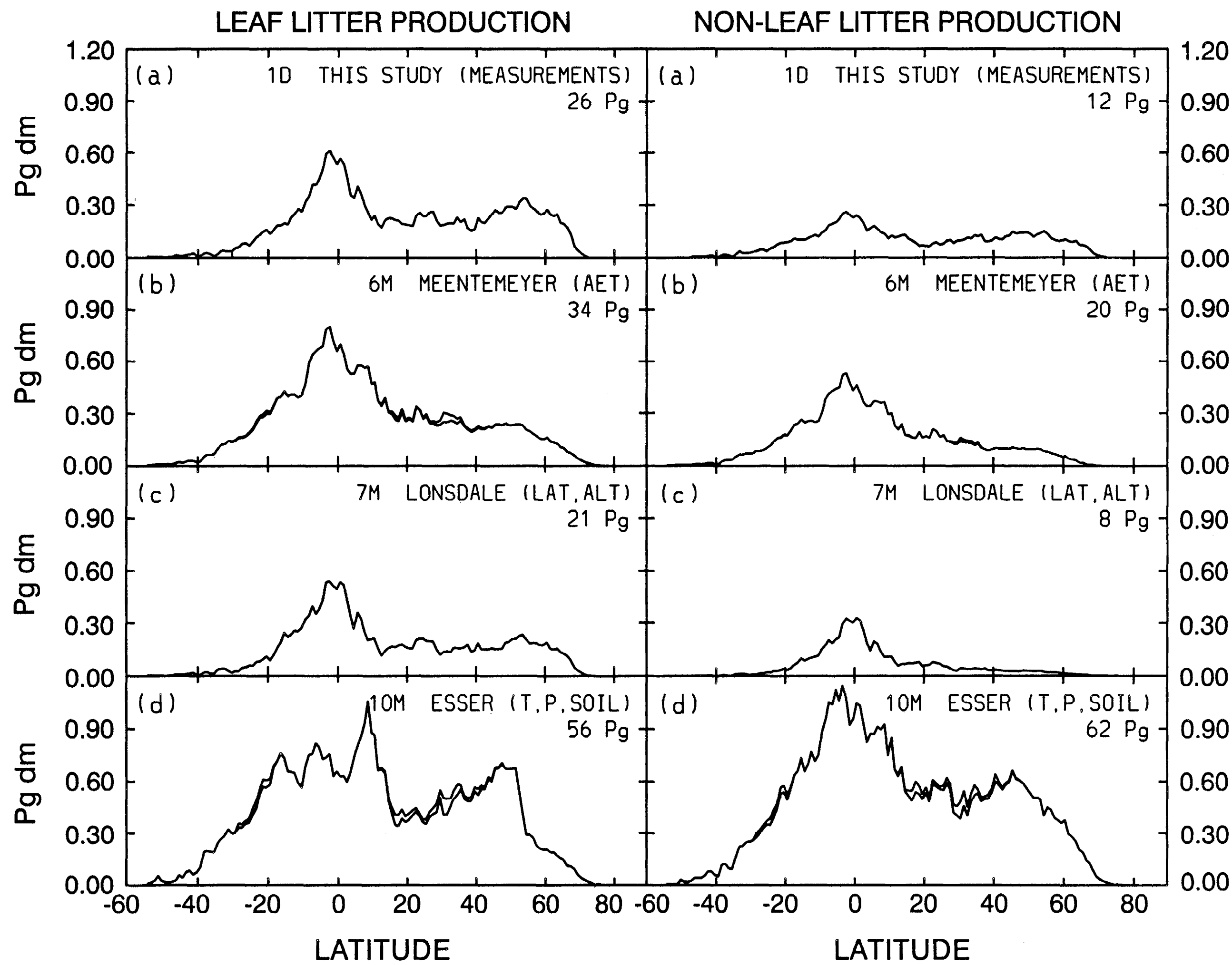

Figure 3. Same as Plate 3 except parameter is 1° total zonal production of litter components: (left) leaf litter, (right) non-leaf or other production. Light lines are values using models directly; heavy lines are the same except deserts are set to zero.

2e) is bimodal with a broad tropical peak extending from 10°S to 15°N, and a broader and slightly lower north temperate peak extending from 35°N to 70°N. Extensive areas of tropical forests are characterized by high extremes in density (Plate 2e) about twice those from the measurement compilation (Plate 2a and Table 5). Abrupt large-scale changes and spotty interspersing of values result from the association of single litter values over entire distributions of vegetation types.

Ecosystem means derived from the measurements (1D in Table 5) are generally lower than those from other techniques and <50% those of *Ajtay et al.* [1979]. The cause of these discrepancies is not clear. *Ajtay et al.* [1979] do not define litterfall, so their values may reflect both aboveground and belowground production while the measurement compilation reflects only aboveground litter. However, information on underground production would have been as scarce in the late 1970s as it is now. *Ajtay et al.* [1979] may have increased aboveground values to account for belowground production in their study. Alternatively, inclusion of some coarse woody litter would have elevated *Ajtay et al.'s* [1979] composites, although this is inconsistent with short litter turnover times estimated from these data (section 5).

Leaf and non-leaf (presumably wood) production was computed by using measurement sites for which both total and leaf measurements are reported (Table 4b). In order to reflect relationships between leaf and total litter from measurements displaying large variability in absolute values, ratios of leaf:total production were calculated for each site and were used to determine mean ratios for ecosystems. These ratios were applied to distributions of total litter to distinguish leaf and "other" production components. Note that 188 measurement pairs of unequal ecosystem representation were used in the estimate (Table 4b).

Geographic distributions of leaf and non-leaf production from the measurements is shown in Plate 3a; zonal totals are shown in Figure 3a. On the basis of these measurements, mean leaf litter production is ~265 g dm/m^2/yr for the forests and woodlands represented in the measurements and the global mean proportion of leaf:total production is 0.67. Leaf fractions for most forests and woodlands are 0.70-0.75 (types 1-11), wooded grasslands (types 23-25) are 0.5-0.6, and sclerophyllous mediterranean forest (type 6) is 0.54. This trend of decreasing leaf fraction with increasing aridity is ecologically reasonable although the ratios seem somewhat high.

3.1.2. Indirect approaches. In this study we employed *Raich and Schlesinger's* [1992] soil respiration measurements to estimate litter production. In their study, the difference between SR and RR is assumed to be SOM input, and turnover times of soil carbon were computed by dividing soil carbon pools by the carbon inputs. In contrast, we consider SR-RR to be an estimate of total (aboveground and belowground) litter production.

As described above, SR is the sum of root respiration, decomposition of aboveground litter and decomposition of SOM described by

$$SR = RR + D_A + D_{SOM} \tag{1}$$

where SR is soil respiration, RR is root respiration, D_A is decomposition of aboveground litter, and D_{SOM} is decomposition of soil organic matter. Since D_{SOM} is dominated by the current year's belowground litter production, we assume that D_{SOM} approximates belowground litter decomposition, D_B, and that decomposition of older SOM is negligible, so that

$$D_{SOM} = D_B \tag{2}$$

and

$$SR = RR + D_A + D_B \tag{3}$$

Total decomposition, D_{TOTAL}, is the sum of aboveground and belowground decomposition, and total production, P_{TOTAL}, is the sum of aboveground and belowground production. Furthermore, under steady state, total litter decomposition equals total litter production so that

$$D_A + D_B = P_A + P_B \tag{4}$$

$$SR = RR + P_A + P_B \tag{5}$$

By isolating the contribution of RR to SR we approximate total litter production:

$$SR - RR = P_{TOTAL} \tag{6}$$

Distributions of litter production were developed by applying ecosystem-specific RR:SR ratios to two distributions of SR based on the work of *Raich and Schlesinger* [1992]. The first (3D), a data-based estimate using SR composites extrapolated with the vegetation data of *Matthews* [1983], is discussed here. (The second, using a climate-based SR regression from the same authors is discussed in section 3.2.3.). Zonal totals for SR and RR are shown in Figure 4a; distributions are shown in Plate 4a. The resulting estimate of litter production is presented in Plate 2b, Figure 2b, and Table 5.

Using the composites, annual SR totals 144 Pg dm with a mean land value of ~1100 g dm/m^2/yr. Root respiration is assumed to contribute about 40% to SR for most forests and 20-30% for grasslands and shrublands [*Peterjohn et al.*, 1993], which gives a mean land value of ~400 g dm/m^2/yr for RR and accounts for 51 Pg dm of annual SR. The balance, litter production, is 93 Pg dm/yr (3D in Table 5 and Plate 2b) equal to ~700 g dm/m^2/yr. Zonal production shows a bimodal distribution with modest peaks centered around the equator and 50°N separated by a trough in the arid subtropical zone (Figure 2b). Tropical values are ~1400-1600 g dm/m^2/yr; values for other forests and woodlands are about half those of the tropics, and grasslands and tundra are <200 g dm/m^2/yr (Plate 2b). With respect to individual ecosystems, the SR-RR means are generally similar to the *Ajtay et al.* [1979] composites, and ecosystem means from both of these methods are considerably higher than means derived from the measurements. This relationship with the measurements is expected since the latter reflect aboveground production. The global total from this SR-RR production estimate is in the low to middle range of reported values from other direct and indirect methods (Table 1b).

We recognize that this SR-RR estimate is very simple. However, the approach has the advantage of capturing both aboveground production, and belowground production in the form of fine roots that turn over in 1 year. Belowground pro-

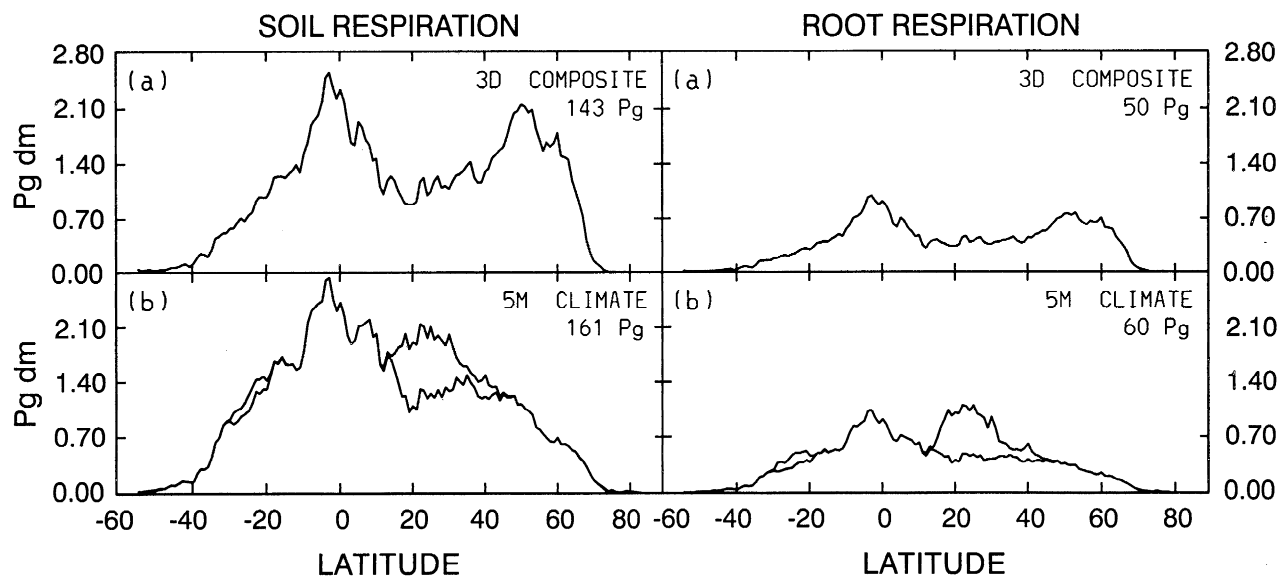

Figure 4. Same as Plate 4 except parameter is 1° zonal total (left) soil respiration and (right) root respiration. Light lines are values using models directly; heavy lines are the same except deserts are set to zero.

duction is difficult to measure and rarely included in litter measurements.

The litter production estimates discussed so far do not take into account production of coarse woody detritus. Such an evaluation is problematic since measurements of any kind are scarce [*Harmon et al.*, 1986]. The global distribution of coarse woody detrital production was developed in this study following closely the technique proposed by *Harmon and Hua* [1991] and *Harmon et al.* [1993]. The estimate is meant to suggest the magnitude of annual CWD production in the context of other litter production values. Briefly, CWD production is estimated from the aboveground live wood biomass pool, and input rates from normal and catastrophic mortality. The live wood biomass pool is defined as a fraction of total biomass, where fractions vary by ecosystem. Total biomass values for vegetation types used here are generally those of *Matthews* [1984], except that tropical values are reduced following the work of *Brown et al.* [1989] and *Brown and Lugo* [1992]. Live wood is generally 80-95% of live aboveground biomass in forests.

Annual production of CWD from normal mortality is given for major forest types relative to live wood biomass [*Harmon et al.*, 1993]; mortality rates are 0.22% (tropical open), 0.43% (cold conifer), 0.64% (warm deciduous), 0.87% (cold deciduous), 0.95% (warm conifer), and 1.58% (tropical closed). Annual CWD input from catastrophic events is estimated as a fraction of live wood biomass and return intervals of catastrophic events, which are given as 1-2 centuries for boreal forests, 2-5 centuries for temperate evergreen forests, 7-15 centuries for tropical forests, and 10-15 centuries for temperate deciduous forests. We used mean intervals for ecosystems.

Harmon et al.'s [1993] global estimate of production from normal mortality is ~7.6 Pg dm/yr with a range of 2.4-18.2 Pg dm; they estimate catastrophic input to be 1.7-3.6 Pg dm/yr, using upper and lower return intervals for catastrophic events, giving a total annual CWD production of 4-22 Pg dm. In this study, total CWD production is estimated to be 12 Pg dm/yr, mostly from normal mortality; forests average ~200-400 g dm/m^2/yr (Table 5). The geographic distribution of CWD production is shown in Plate 2d, and zonal totals are shown in Figure 2d (note the unique scale for Plate 2d and Figure 2d). Highest production is in tropical forests for which measurements are scarce. Temperate/boreal needleleaved forest (type 8) and temperate deciduous forests (types 10-11) are similar, close to 200 g dm/m^2/yr respectively. Boreal needleleaved woodland (type 14) is 120 g dm/m^2/yr, and boreal deciduous woodland (type 16) is ~95 g dm/m^2/yr. Total production is concentrated in the tropics with a secondary peak at 50°-65°N (Figure 2d). Measurements reported by *Harmon et al.* [1986] suggest CWD production rates of ~220 g dm/m^2/yr for all coniferous forests, which decline to ~80 g dm/m^2/yr when measurements of anomalous western evergreen rainforests are removed; production is ~90 g dm/m^2/yr for deciduous forests. Considering the very large variations in the measurements, this agreement is considered encouraging.

Several reported indirect estimates of litter production (i.e., NPP) based on composited published data are noted in Table 1b. They range from 89 to 120 Pg dm/yr. The data of *Fung et al.* [1983] were developed from the same vegetation data base used in this study, and NPP varies with latitude and ecosystem. The distribution resembles the pattern of litter production from ecosystem composites of *Ajtay et al.* [1979] (Figure 2e) although the tropical peak in the *Fung et al.* [1983] distribution is more pronounced.

3.2. Model-Based Production Estimates

3.2.1. Direct approaches. We implemented the regression models of *Meentemeyer et al.* [1982] and *Lonsdale* [1988] which predict litter production from climate, and from elevation and latitude, respectively.

The model of *Meentemeyer et al.* [1982], based on five temperate sites, estimates the production of leaf litter and total litter from actual evapotranspiration (6M in Table 2). Global density of total litter production is shown in Plate 2f, latitudinal totals are shown in Figure 2f, and ecosystem means are shown in Table 5.

When *Meentemeyer et al.'s* [1982] model is implemented, total litter production is 54 Pg dm annually, of which leaf litter is 34 Pg. (The authors did not compute global values.) The relative contribution of leaf to total litter, ~65%, is consistent with the measurement compilation although magnitudes of both are small, indicating that only aboveground production is included. The geographic distribution of litter production (Plate 2f) reflects primarily the Earth's temperature regime, with some east-west variations introduced by precipitation. The abrupt boundaries exhibited in composite-based distributions (e.g., Plate 2e) are smoothed by modeling litterfall from factors that vary gradually over landscapes. Density maxima in the tropics reach >1200 g dm/m^2/yr, similar to several other distributions in Plate 2. However, arid zones and many areas throughout temperate latitudes to the poles have values at the low end of the scale (<180 g dm/m^2/yr). Non-arid temperate regions are characterized by intermediate densities of ~180-600 g dm/m^2/yr and most tropical and subtropical forests produce ~850-1100 g dm/m^2/yr of litter. The single tropical peak in the zonal totals (Figure 2f), characterized by values of 900-1620 g dm/m^2/yr (Plate 2f), declines to a plateau ±15° of the equator. Humid temperate regions in the northern and southern hemispheres exhibit production values in the range of 270-720 g dm/m^2/yr, and drier temperate and boreal regions are ≤270 g dm/m^2/yr. Deserts contribute little in this model. As expected, zonal sums for the distributions exhibit modest tropical peaks and temperate values about one third those in the tropics (Figure 2f).

The model of *Meentemeyer et al.* [1982] also allows an estimate of leaf and non-leaf litter production, shown in Figure 3b. Leaf production is concentrated in the tropics with a broad plateau from 20°N to 60°N, equal to half the tropical highs. With the exception of the bulge from 50°-60°N in the measurement distribution (Figure 3a), latitudinal trends of these two techniques are similar for leaf litter production.

The inverse relationship between climate and litter production is exploited in a simple model proposed by *Lonsdale* [1988] which estimates total litterfall in forests from latitude and elevation, and leaf litterfall in forests from latitude only. The model was developed from measurements at 88 forest sites although information on the measurements is not provided. Distributions of total forest litterfall are shown in Plate 2g and Figure 2g; leaf and non-leaf components are shown in Figure 3c. *Lonsdale* [1988] does not report global totals, but implementing the model with the modified Rand topographical data [*Gates and Nelson*, 1974] and a forest/woodland mask from the vegetation data set, gives 29 Pg dm/yr for total forest litterfall; the leaf component is 72% (21 Pg dm). The impact of elevation on production of leaf litter production is minor at this resolution. Because the *Lonsdale* [1988] model applies only to forests, this result should be, and is, most similar to

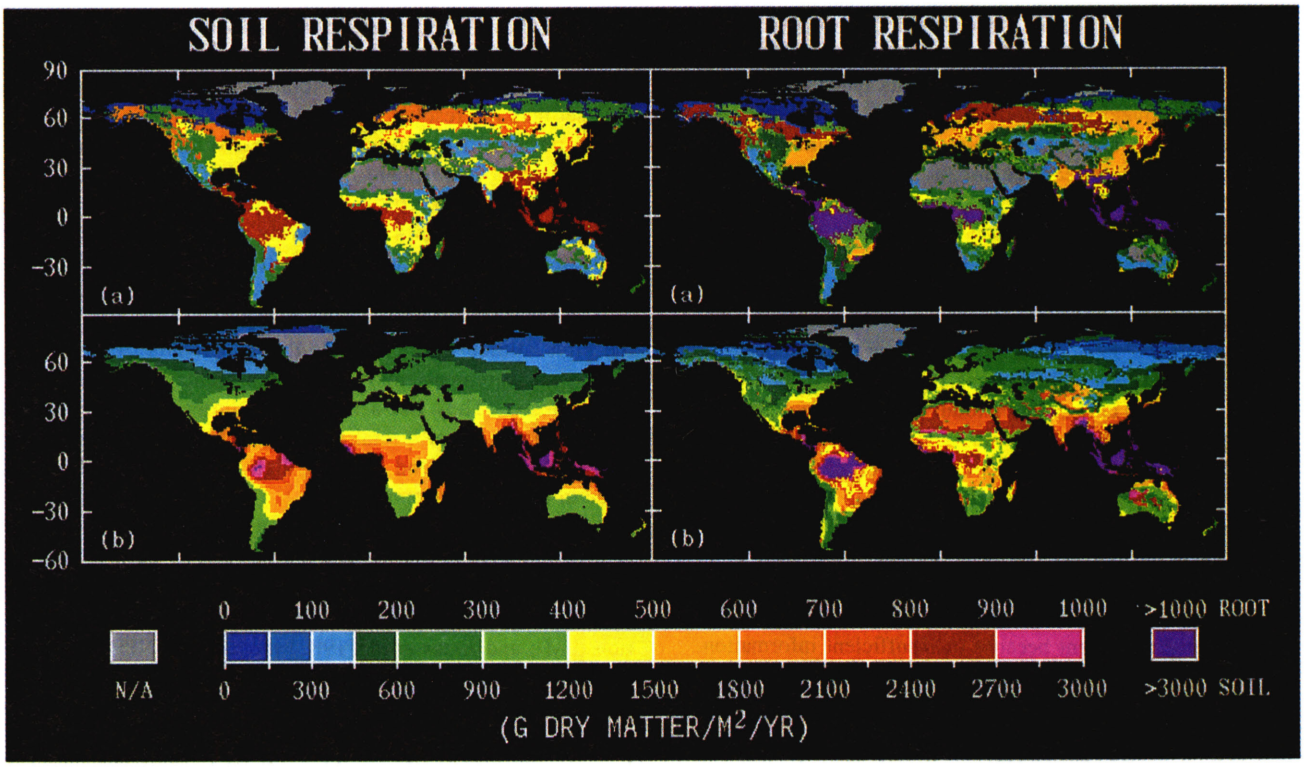

Plate 4. Geographic distribution of SR (left panels) and RR (right panels) from *Raich and Schlesinger* [1992]: (a) 3D, SR and RR from ecosystem composites; (b) 5M, SR modeled from climate, RR from ecosystem composites.

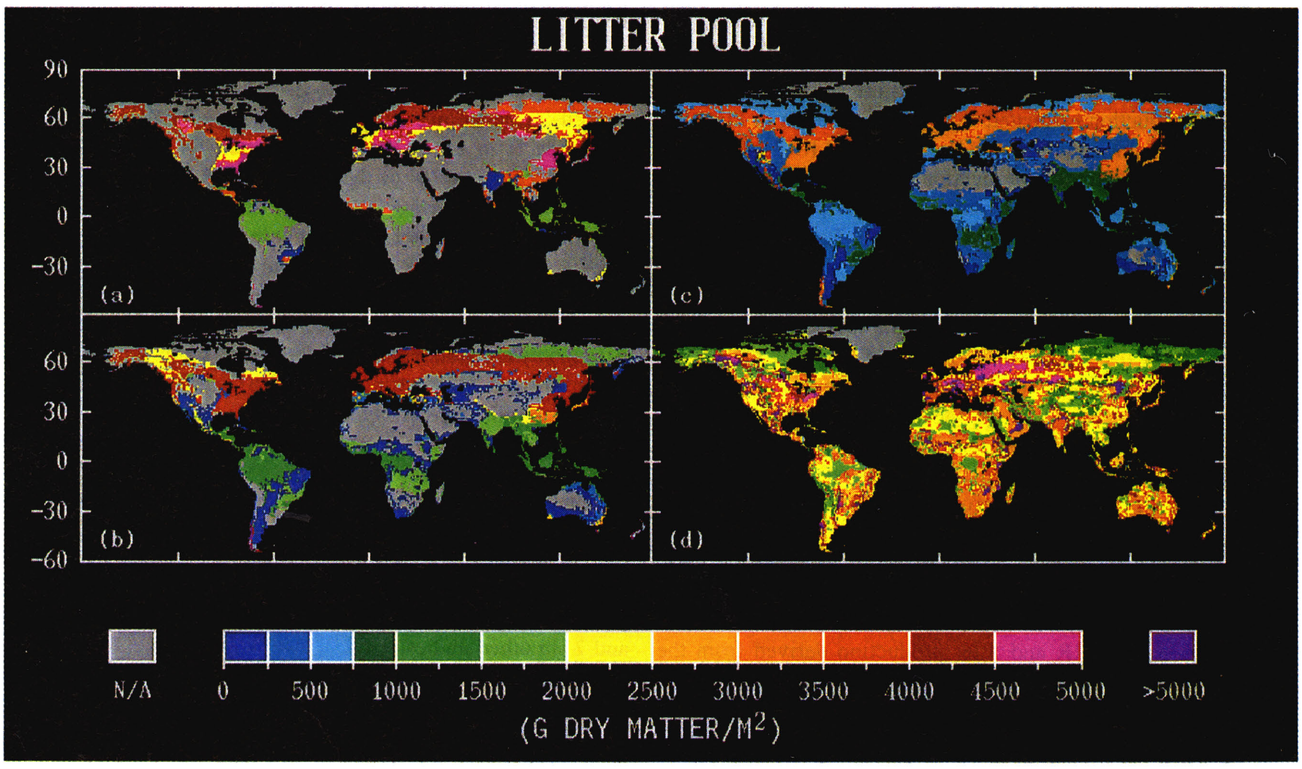

Plate 5. Geographic distribution of litter pools: (a) 1D, this study, measurement compilation; (b) 4D, this study, coarse woody detrital pool; (c) 2D, ecosystem composites of *Ajtay et al.* [1979]; (d) 10M, total litter pool of *Esser et al.* [1982] modeled from NPP and decomposition.

the measurement compilation (compare Plates 2a and 2g, and Figures 2a and 2c). The low total, along with the fact that the model relies on litter measurements which probably do not reflect belowground production, suggests that this model considers only aboveground production. In fact, the measurement and Lonsdale distributions are discouragingly similar considering the major effort required for the measurement-based estimate.

By way of comparison, annual litterfall from the model of *Goudriaan and Ketner* [1984] is 85 Pg dm; a related model [*Rotmans and DenElzen*, 1993] reports 95 Pg dm, only 48% of which is leaf litter (Table 1b). Since information on the geographic distribution of these predictions is unavailable, further comparison with the distributions presented here is not possible although the latter higher totals are consistent with those expected when both aboveground and belowground production are included. However, the low contribution of leaf litter to the total reported in *Rotmans and DenElzen* [1993] is not consistent with the inclusion of underground (fine root) detritus unless they consider fine roots as non-leaf or woody material. If, however, non-leaf production is exclusively woody, the low leaf fraction is difficult to explain. These speculations cannot be confirmed at present because of insufficient information.

3.2.2. Indirect approaches. The four indirect litter production estimates presented here employ soil respiration and net primary productivity as proxies for litter production. One estimate introduced above (3D) assumes litter production equal to SR minus RR, where the SR distribution is derived by extrapolating ecosystem composites [*Raich and Schlesinger*, 1992]; this section describes a hybrid technique (5M) in which the SR distribution is predicted from climate [*Raich and Schlesinger*, 1992] and, as before, root respiration is estimated as a fraction of SR and varies by ecosystem. The other three estimates (8M-10M) model NPP from climate.

Zonal totals of climate-derived distributions of SR and of RR are shown in Figure 4b; distibutions are shown in Plate 4b; and litter production estimated from them is shown in Plate 2c. SR modeled from climate is 160 Pg dm/yr, and RR is 60 Pg dm (Figure 4b), giving litter production as 100 Pg dm (Plate 2c, Figure 2c, and Table 5). By contrast, the composited estimates from *Raich and Schlesinger* [1992] are 144 Pg dm for SR and 51 Pg dm for RR (Figure 4a), giving 93 Pg dm for litter production (Plate 2b, Figure 2b, and Table 5).

Global mean SR derived from climate is about 10% higher than that from the composites. However, most of the excess SR occurs in non-vegetated desert, which accounts for the subtropical discrepancies between the data sets. Total SR estimated with these two approaches is essentially equal when desert areas are eliminated in the regression (area under the heavy line in Figure 4b). Xeromorphic formations (types 12 and 21) account for 9% of total SR in the climate-based estimate, and appear to have anomalously high SR values (1600 and 1000 g dm/m^2/yr, respectively) similar to those of forests, woodlands, and grasslands. Therefore, although total SR from climate, as well as RR and litter production derived from the distribution, is ~10% higher than that from the composites, relationships between the two techniques vary with latitude (Figures 2b, 2c, and 4). Tropical peaks in all three parameters are similar between the two methods. However, while subtropical values (10°-30°N) for the climate-based distributions are consistently higher because SR is overestimated in arid regions, composited estimates of SR, and therefore of RR and litter production, are consistently higher in high-latitude zones of the northern hemisphere, probably because SR for temperate/subpolar needleleaved forest (type 8) is about 3 times SR from climate. One explanation is that the vegetation data set may not resolve gradual zones of declining tree density in the northward transition from forest to tundra, particularly in the eastern hemisphere. The location of such boundaries conflicts among land-cover data sets [*DeFries and Townshend*, 1994]. On the other hand, deriving measurement means for ecosystems is not exact and alternative groupings of the measurements would change the ecosystem means extrapolated with the vegetation data. Another possible explanation for the high-latitude discrepancy is that *Raich and Schlesinger's* [1992] measurements may not be representative of high latitude forests. They list a total of 16 boreal forest/woodland measurements out of a total of ~170: four in the former USSR at 64°N, one in Finland at 66°N, eight in Alaska at 64°N, and three in European swamp forests.

The three regression models predicting NPP from climate rely on an assumption of ecosystem steady state (Table 2). *Rosenzweig* [1968] models aboveground NPP from AET (8M); *Lieth* [1975] models total NPP from temperature and precipitation (9M); and *Esser et al.* [1982] model total NPP from temperature, precipitation, and soil factors (10M). (Note that the early version of Esser's model used here does not reflect that model's current sophistication. Later versions includes soil organic production, leaching from soil, transient land-use changes, and inputs from fossil fuels.)

Since the model of *Rosenzweig* [1968] predicts aboveground NPP, it was expected to give a low estimate in relation to other NPP totals (Table 1b) and ecosystem means resembling those based on the measurements (Table 5). Nonetheless, implementing *Rosenzweig's* [1968] model gives a global production value of 139 Pg dm/yr (Tables 2 and 5) which is the upper bound for reported total NPP and for litter production. The latitudinal distribution is very strongly peaked in the tropics (Figure 2h) where NPP for much of the land area is in excess of 1800 g dm/m^2/yr (Plate 2h). The abrupt decline at ±10° of the equator leads into a more gradual decline from 10° to 50° in the southern hemisphere while the decline in the northern hemisphere plateaus from ~30° to 60°N. As in the work of *Meentemeyer et al.* [1982], deserts play a minimal role in the distribution. The geographic distribution shows very strong gradients in the southeast US, in Africa outward from equatorial forests, in south Asia, and along the east coast of Australia (Plate 2h). Litter production for tropical humid forests (types 1 and 2) and tropical drought-deciduous forest (type 9) are higher than most other estimates by a factor of 3-4 (8M in Table 5). The climate-based SR-RR estimate (5M) shows similar relationships among these tropical forests but the magnitudes are much lower. Litter production in xeromorphic and sclerophyllous woodlands (types 12 and 13) from *Rosenzweig's* [1968] model are ~1800 and 1000 g dm/m^2/yr, respectively, similar to tropical forests (types 1 and 2) in other studies.

Successive generations of what is now the HRBM of *Esser et al.* [1994] trace their lineage to the Miami model of *Lieth* [1975] which models NPP from annual mean temperature and from annual total precipitation and takes the minimum. The Hamburg model of *Esser et al.* [1982] and *Esser* [1987] extended the Miami formulation to include the effect of soil fertility as well as allocation of NPP to herbaceous and woody compartments; the latter translates into herbaceous and woody litter production under steady state. According to *Esser et al.* [1982], soil factors were introduced to improve (reduce) NPP estimates in arid regions modeled exclusively from climate, i.e., the Miami model. Soil effects are included by associating soil factors, ranging from 0.04 for a takyric solonchak to 2.78 for a gleyic luvisol, with FAO soil types. These multiplicative factors introduce fertility effects by modulating the climatically-derived NPP values; the logic is that the difference between potential NPP as governed by climate and that observed is due to the local influence of soil fertility. We used *Zobler's* [1986] digital version of the FAO soil map to incorporate the influence of soil fertility into the estimate of total NPP. Herbaceous and woody fractions defined for vegetation types from *Esser et al.* [1982] were associated with the *Matthews* [1983] vegetation types to allocate litter production.

Implementing the Miami model gives total NPP or litter production of 131 Pg dm/yr (9M in Table 5) in the upper range of reported NPP values (Table 1b). NPP from the Hamburg model [*Esser et al.*, 1982] is 118 Pg dm (10M). The geographic distribution from *Lieth* [1975] (Plate 2i) closely resembles that of *Rosenzweig* [1968], although Lieth's values are lower for some tropical ecosystems and higher for north temperate regions in western and eastern Europe (Table 5). Zonal similarities between *Lieth* [1975] (Figure 2i) and *Esser et al.* [1982] (Figure 2j) mask the speckled distribution introduced by the soil data (Plate 2j).

The tropical peaks from *Lieth* [1975] (Figure 2i) and *Esser et al.* [1982] (Figure 2j) are less pronounced than the one from *Rosenzweig* [1968] (Figure 2h) but more pronounced than those from the *Ajtay et al.* [1979] composites (Figure 2e) and from the SR-RR distributions (Figures 2b and 2c). *Esser et al.'s* [1982] Hamburg values for desert (type 30) and for xeromorphic shrubland (type 21) are lower than those of Lieth [1975] as are the Hamburg estimates for many forests (types 1-11) although several other xeromorphic formations (e.g., types 12 and 25) are somewhat higher in the Hamburg model.

Zonal totals for leaf and woody litter production from *Esser et al.* [1982] are shown in Figure 3d. Most striking is the equality of herbaceous and woody litter; herbaceous litter accounts for 48% and woody litter for 52% of total production. In contrast, most other estimates (Tables 1b and 2), as well as the measurements, suggest that leaf litter contributes somewhat more to total fine litter production. In comparing ecosystem means among studies, woody production values from *Esser et al.* [1982] are consistently higher by a factor of 2-5 or more than means from other methods (9M in Table 5). Because woody components decompose more slowly than foliar materials, this large woody production substantially enhances the pool size and turnover time. This influence is pervasive but particularly evident in arid areas.

Terrestrial ecosystem models include NPP modeled from methods of varying sophistication. Table 1b shows a suite of modeled NPP totals. Reported total NPP ranges from 84 Pg dm/yr [*Bonan*, 1995] to 135 Pg dm/yr [*Box et al.*, 1988]. Modeled distributions of zonal NPP are available for three models [*Fung et al.*, 1987; *Box*, 1988; *Ruimy et al.*, 1994]; the latitudinal totals from *Box* [1988] are similar to those of *Lieth* [1975] (Figure 2i) where the tropical peak dominates and temperate values are about half those in the tropics. NPP from *Ruimy et al.'s* [1994] model exhibits an entirely different distribution, with temperate regions contributing more than the tropics to the global total. *Ruimy et al.'s* [1994] high conversion efficiencies of energy to dry matter in cultivated land partially explain this difference, but the general pattern persists even when only natural vegetation is used. Litter production from *Box* [1988], 135 Pg dm/yr, is the highest of all the approaches reported in Table 1b.

3.3. Litter Production Discussion

Although it is often difficult to determine whether models or measurements include both aboveground and belowground litter production, totals for direct model-based estimates (Table 1b) suggest that only aboveground production is included or that litter production includes some combination of aboveground and belowground. Results of indirect model-based approaches using NPP as a proxy are generally higher than direct model-based and data-based litter values because the NPP estimates include aboveground and belowground production. The indirect approaches using SR-RR as a production proxy are intermediate between those using NPP and those estimating litter production directly. The SR-RR approaches presented here are 93 and 100 Pg dm/yr based on composites and climate, respectively.

The fraction of litter production that occurs belowground can be assessed in a general way by comparing aboveground measurements (1D) to the SR-RR approaches (3D and 5M) despite the fact that they are not entirely compatible. Litter production from the measurements is 39 Pg dm for the 97 x 10^{12} m^2 of wooded ecosystems represented by the measurements. Using the SR-RR approach gives a litter production of 79 Pg dm for the same wooded areas, suggesting that belowground production averages about 50%, with a range of ~20-80%, of the total for these ecosystems. This value is consistent with the data of *Vogt et al.* [1986] who report that belowground litter production in the form of fine roots is ~55-60% of total litterfall in several warm and cold temperate forests, and ~40% of the total in boreal evergreen forests. Belowground production for wooded grasslands is 69%, 83%, and 52% of the total for types 23, 24, and 25, respectively, when the measurements are compared with composited SR-RR production, and 74%, 87%, and 63% when compared with climate-based SR-RR production. The comparisons for shrublands are intermediate but difficult to interpret.

These relationships between forest/woodland types and grasslands are generally consistent with below-to-aboveground ratios of NPP reported by *Ruimy et al.* [1994], although the ratios themselves are somewhat higher than *Ruimy et al.'s* [1994] for forests/woodlands (0.3-0.6 for this study versus 0.1-0.4 for *Ruimy et al.* [1994]) as well as for grasslands (2-6 for this study versus a mean of 2.8 [*Ruimy et al.*, 1994]). Despite consistency in general relationships, mean ratios for ecosystems are underlain by a wide range of ratios for individual ecosystems (this study) and for individual study sites [*Ruimy et al.*, 1994]. For instance, *Ruimy et al.* [1994] report ratios of below-to-above NPP that vary by a factor of 3 for mixed forests, a factor of 5 for grasslands, and a factor of 6 for tropical forests.

Raich and Schlesinger's [1992] indirect estimate for the upper bound for NPP, after consideration of herbivory, fire, and RR, is in the range of 90-110 Pg dm/yr. High NPP totals of 135 Pg dm/yr [*Box*, 1988], 134 Pg dm/yr [*Goudriaan and Ketner*, 1984], 129 Pg dm/yr [*Warnant et al.*, 1994], 124 Pg dm [*Foley*, 1994], and 121 Pg dm [*Rotmans and DenElzen*,

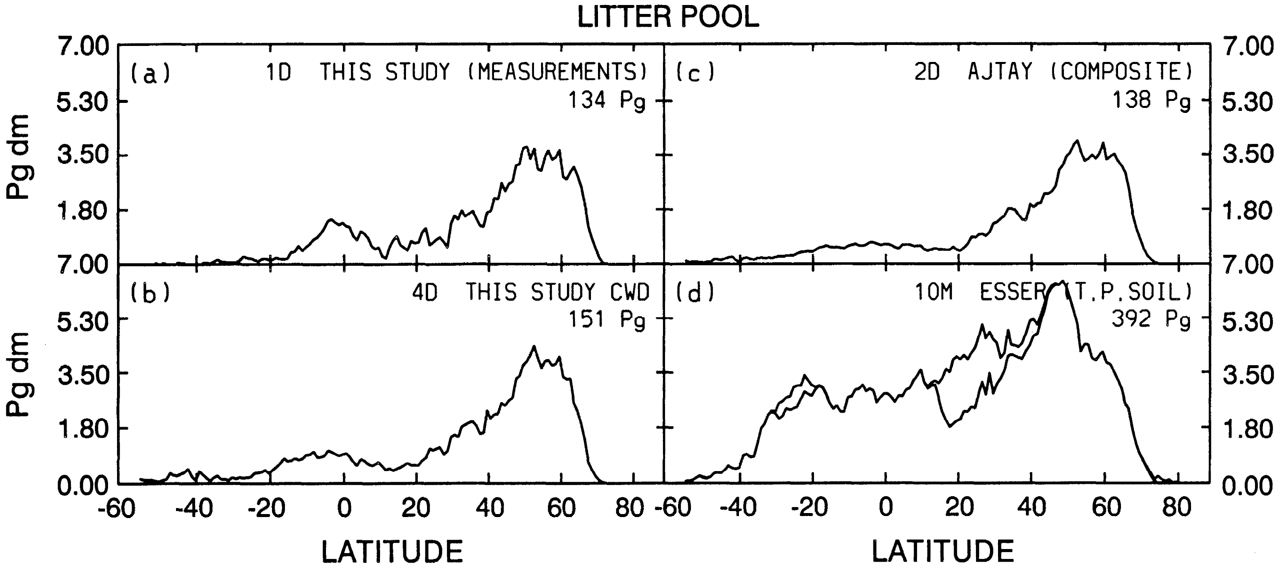

Figure 5. Same as Plate 5 except parameter is 1° zonal total litter pool. Light lines are values using models directly; heavy lines are the same except deserts are set to zero.

1993] (Table 1b) are inconsistent with this upper value for NPP and, by inference, for litter production. The litter measurement compilation in this study, albeit partial, suggests the lower range for NPP, consistent with the soil respiration data presented by *Raich and Schlesinger's* [1992] and used in this study.

4. Litter Pool

Although many models characterize the dynamics of input, decay, and transfer of litter material among pools of organic matter, the definition of pools is often vague. Because it is loosely defined in models and difficult to determine in the field, the size, composition, and distribution of the litter pool are poorly constrained. In addition, the surface litter pool can sometimes be included as part of SOM (as in the model of *Meentemeyer et al.* [1985]) although it is not included in *Post et al.'s* [1982, 1985] soil carbon profiles.

This study includes four global distributions of the litter pool. Geographic distributions are shown in Plate 5; zonal totals are shown in Figure 5; and ecosystem values are shown in Table 6. Three of the estimates reflect the fine litter pool (1D, 2D, and 10M); the fourth is the coarse woody pool (4D).

4.1. Data-Based Pool Estimates

4.1.1. Direct approaches. Despite ambiguity surrounding the term, several hundred litter pool measurements have been published for forests [e.g., *Vogt et al.*, 1986; *Brown and Lugo*, 1982]. Composite litter pool or littermass values have also been published for ecosystems [*Reiners*, 1973; *Whittaker and Likens*, 1975; *Ajtay et al.*, 1979]. We developed two data-based estimates of the global litter pool. One relies on the measurements compiled for this study and the other is based on ecosystem composites of *Ajtay et al.* [1979] (1D and 2D, respectively, in Table 2). The measurement-derived and composite-derived distributions are shown in Plates 5a and 5c, respectively; zonal totals are shown in Figures 5a and 5c, respectively; and ecosystem means are listed in Table 6.

The partial measurement estimate and the global composite-based litter pool estimate are very close: 136 Pg dm versus 138 Pg dm, respectively. However mean litter pool for wooded ecosystems represented in the measurements is ~2100 g dm/m^2, while that from *Ajtay et al.* [1979] is ~1500 g dm/m^2 for the same suite of wooded ecosystems. Because means for temperate and boreal forests (types 8, 10, and 11) are within 30% of each other, and values for boreal cold-deciduous woodland (type 16) are very similar in the two estimates, the structure and magnitude of the zonal totals are similar north of 50°N (Figures 5a and 5c). However, tropical and subtropical distributions diverge substantially. Measurements suggest pool values for tropical rainforests (type 1) ~2.5 times those proposed by *Ajtay et al.* [1979] (Table 6) . Although tropical soils have historically been considered low in SOM due to rapid decomposition rates, *Nepstad et al.* [1994] report soil carbon pools in tropical forests larger than previously believed, suggesting that these high measurement values may reflect conditions in some tropical environments. Discrepancies are apparent for most of the remaining forests (types 2 and 6-11). Overall, the north temperate/boreal values from the measurements (Plate 5a) bracket those derived from *Ajtay et al.* [1979] for the same regions. Because of high measured values for tropical/subtropical evergreen broadleaved forest (type 2 in Table 6), Figure 5a shows a secondary tropical peak absent in results based on *Ajtay et al.* [1979](Figure 5c).

There are several possible explanations for these discrepancies. The measurements are unevenly distributed among ecosystems; filling data gaps may alter ecosystem means derived from the measurements. Alternatively, the association of measurement site descriptions with vegetation types is open to interpretation. On the other hand, tropical litter pools may be larger than they were previously understood to be.

Section 3.1.2. describes estimation of the live wood biomass pool to evaluate annual production of CWD [*Harmon and Hua*, 1991]. These authors also outline a technique to estimate the pool of coarse woody detritus based on measured relationships between the CWD pool and live wood biomass. They report ratios of CWD to live wood biomass of 5% for

Table 6. Litter Pool by Vegetation Type

Vegetation Type	Area 10^{12} m^2	Data-Based 1D This Study Measurem.	2D Ajtay Composites	4D This study CWD	Model-Based 10M Esser T, P, Soil
1	12.8	1537	650	1060	2686
2	4.1	3600	850	1060	2949
3	0.2	...	650	1060	3724
4	0.4	...	3500	7460	4255
5	1.2	...	3000	3160	3451
6	0.6	2002	500	2700	3973
7	0.5	1852	850	2140	3243
8	9.5	4288	3500	4140	3483
9	4.0	208	850	1640	3358
10	7.7	4605	3000	4040	3789
11	5.5	2050	3000	4040	3728
12	3.1	...	100	180	3317
13	2.3	...	500	440	3366
14	2.6	...	3500	2480	3673
15	4.7	...	850	1740	3555
16	2.6	3702	3500	1720	1912
17	1.6	...	100	220	3042
18	0.7	...	2500	220	3108
19	1.0	...	100	220	3087
20	0.5	...	500	220	2520
21	9.4	...	100	40	2861
22	7.2	...	700	...	1885
23	8.5	...	350	180	3008
24	4.2	...	350	60	2909
25	10.7	...	350	...	3293
26	1.5	...	500	...	2229
27	1.5	...	325	...	2652
28	7.3	...	325	...	2210
29	0.3	...	325	...	1239
30	15.8	...	0	...	2562
Total area	132	47	132	88	132
Total pool		134	138	151	392
Mean pool		2835	1046	1722	2971

Production, except for totals, is g dm/m^2/yr.

tropical rainforests, shrublands, and grasslands, and ~20-25% for subtropical, temperate, and boreal forests. Live biomass and ecosystem ratios of CWD to live biomass applied to the *Matthews* [1983] vegetation data gives a CWD pool of 151 Pg dm similar to the estimate of the fine litter pool (Table 6). The global mean of ~1700 g dm/m^2 (10M in Table 6) is comparable to the measurement-based estimate of ~2100 g dm/m^2 (1D). The zonal distribution of CWD is similar to both the measurement estimate and *Ajtay et al.'s* [1979] composites (compare Figure 5b with Figures 5a and 5c). Tropical values are 1000-2000 g dm/m^2 while most temperate and boreal forests are >4000 g dm/m^2. As with the CWD production estimates, this distribution is considered very uncertain but CWD likely represents a substantial carbon pool.

Reported values for the global litter pool generally do not include standing dead wood or large woody litter. *Ajtay et al.* [1979] estimate 120 Pg dm for live standing biomass, but comment that an additional 40-60 Pg dm may be held in the "dead standing wood" and 10 Pg dm in "dead wood and dry trees," giving a total of 50-70 Pg dm for mostly coarse woody detritus.

4.2. Model-Based Pool Estimates

4.2.1. Direct approaches. We located a single regression model [*Esser et al.*, 1982] that could be implemented to estimate the global litter pool (10M in Table 6). The model of *Meentemeyer et al.* [1985] predicts total detrital carbon, in soils and the overlying litter pool, from climate and disturbance factors but is not included in this study because the soil component dominates and the litter pool cannot be isolated.

Esser et al. [1982] and *Esser* [1987] provide a suite of regression models to evaluate the size and distribution of the global litter pool. In these model versions the herbaceous and woody litter pools are derived from litter production (assumed equal to NPP) and litter decomposition which are modeled primarily from climate. The steady-state litter pool totals 382 Pg dm/yr, with 30% made up of herbaceous litter and 70% comprising woody litter. The global distribution of the combined pool is shown in Plate 5d; zonal totals are shown in Figure 5d, and ecosystem means are presented in Table 6. *Esser et al. 's* [1982] global litter pool is almost 3 times that from *Ajtay et al.'s* [1979] composites. About 10% of the Esser total is in deserts, which have a mean value of ~2600 g dm/m^2. The global terrestrial mean is ~3000 g dm/m^2 and the similarity among ecosystem means is striking (Table 6). These similarities are not entirely due to low variability over the landscape (Plate 5d) but to homogeneous background values overlain with the speckled pattern of soil fertility effects also apparent in litter production (Plates 2j and 3d). The litter pool for much of the world is in the range of 2000-2500 g dm/m^2, declining to ~750-1500 g dm/m^2 in boreal zones, and rising to 3000-3500 in arid subtropics and >4500 in interior Europe and North America.

As with litter production, many ecosystem models evaluate litter pools directly. Table 1a summarizes pool values reported from a series of ecosystem models. Results of the Hamburg model reported by *Esser et al.* [1982], whose implementation is reported here, are included to demonstrate the influence of using different climate and/or soil data sets with the models and the effect of assuming different carbon contents for organic matter components. Nevertheless, the values from Esser are consistently 2-3 times those of most models. Although the sum for fine litter and CWD estimated from measurements approaches that of Esser, there is no indication that inclusion of the CWD component is the cause for such elevated values in the Esser model. For example, ecosystem means for herbaceous environments are the same as those for wooded ones.

Estimates of the global litter pool generally do not include CWD although the values reported for Esser's Hamburg model [*Esser et al.*, 1982] and *Potter et al.'s* [1993] CASA suggest that this woody pool might be included. Reported estimates for total litter pool (Table 1a) vary by a factor of 4, from 84 Pg dm [*Bonan*, 1995] to 382 Pg dm [*Esser et al.*, 1982]. The model of *Rotmans and DenElzen* [1993] is derived from *Goudriaan and Ketner* [1984] which might explain the similarity of those pool totals. More recent values from Esser's HRBM [G. Esser, private communication, 1996] and from CASA [C. S. Potter, private communication, 1996] are about half the estimates reported in Table 1a for earlier versions of those models. Of the CASA total of 348 Pg dm [*Potter et al.*, 1993), 186 Pg dm is composed of leaves and fine roots, a finding that agrees reasonably well with other values for fine litter.

However, the smaller total litter pools in the range of 150-200 Pg dm subsequently estimated with these models are inconsistent with the conjecture that CWD is included. Although it is intriguing that the ~160 Pg dm reported as the woody litter pool for CASA by *Potter et al.* [1993], which "includes everything between leaves and large roots" is extremely close to our estimate of 151 Pg dm for CWD, the latitudinal distribution of the woody pool from CASA and the CWD pool from this study are not compatible (compare Figure 5b versus Figure 8 of *Potter et al.* [1993]). The CWD pool shows a single broad peak in the high temperate/boreal latitude zone from 50° to 70°N while zonal totals in tropical and subtropical regions are generally ~25% of those at high latitudes and temperate regions are about one half those farther north (Figure 5b). CASA shows similar values for high temperate and tropical zones; these strongly peaked regions are separated by a relatively abrupt decline to values about one-third of the others extending from 10°-50° N.

4.3. Litter Pool Discussion

The results of this study suggest that tropical litter pools may be higher than has generally been thought. Furthermore, this initial distribution of the CWD pool suggests that it is comparable in size to the fine litter pool and represents a substantial source of carbon with decadal turnover times. Substantial gaps remain with respect to litter pool measurements for ecosystems such as arid formations and grassland environments, so distributions in these regions remain uncertain.

5. Litter Turnover Time

Steady-state turnover time, in years, is calculated by dividing pool by annual production rate. Figure 6 shows mean zonal turnover times for compatible pairs of pool and production estimates. The family of biosphere models represented by the work of Lieth and Esser are paired to estimate turnover times. Note that the scale for turnover time is 0-30 years for all panels except that for CWD, which is 0-60 years.

The general pattern of turnover times is increasing turnover with distance from the equator. Several prominent exceptions are apparent for the arid subtropics in Figures 6b, 6d, and 6e. The CWD turnover results (Figure 6b) suggest that annual mortality may be underestimated resulting in underestimates of production. Causes for the subtropical result are difficult to interpret because of severe data limitations.

One notable feature of the turnover times shown here s that the pool and production data of *Ajtay et al.* [1979] are internally inconsistent (Figure 6c). The global mean is only 1.4 years despite the fact that the pool total of ~140 Pg dm suggests that wood litter is included. Temperate/boreal evergreen needleleaved forests (type 8) and cold-deciduous woodlands like larch (type 16) have turnover times of only 5.8 and 2.7 years, respectively, for this case. It is likely that the production from *Ajtay et al.* [1979] may be underestimated in northern latitudes, giving an anomalously short turnover time for those latitudes (Figure 2d).

The turnover time for the Esser data pair is 3.4 years (Figure 6e), the same as that reported by *Esser et al.* [1982]. Means are 2.1 yr for the herbaceous pool and 3.4 yr for the woody pool. Although the pool size is very large, suggesting that CWD may be a component, such short turnover times are inconsistent with CWD inclusion. In addition, the wide variety of ecosystems represented here display similar turnover times because both production and pools are relatively homogenous among ecosystems. Most turnover times in both the Esser/Esser pair and the Lieth/Esser pair lie in the range of only 2-7 years. Exceptions are arid regions such as desert (type 30) and xeromorphic shrubland (type 21), along with boreal larch woodland (type 16), which exhibit longer life-

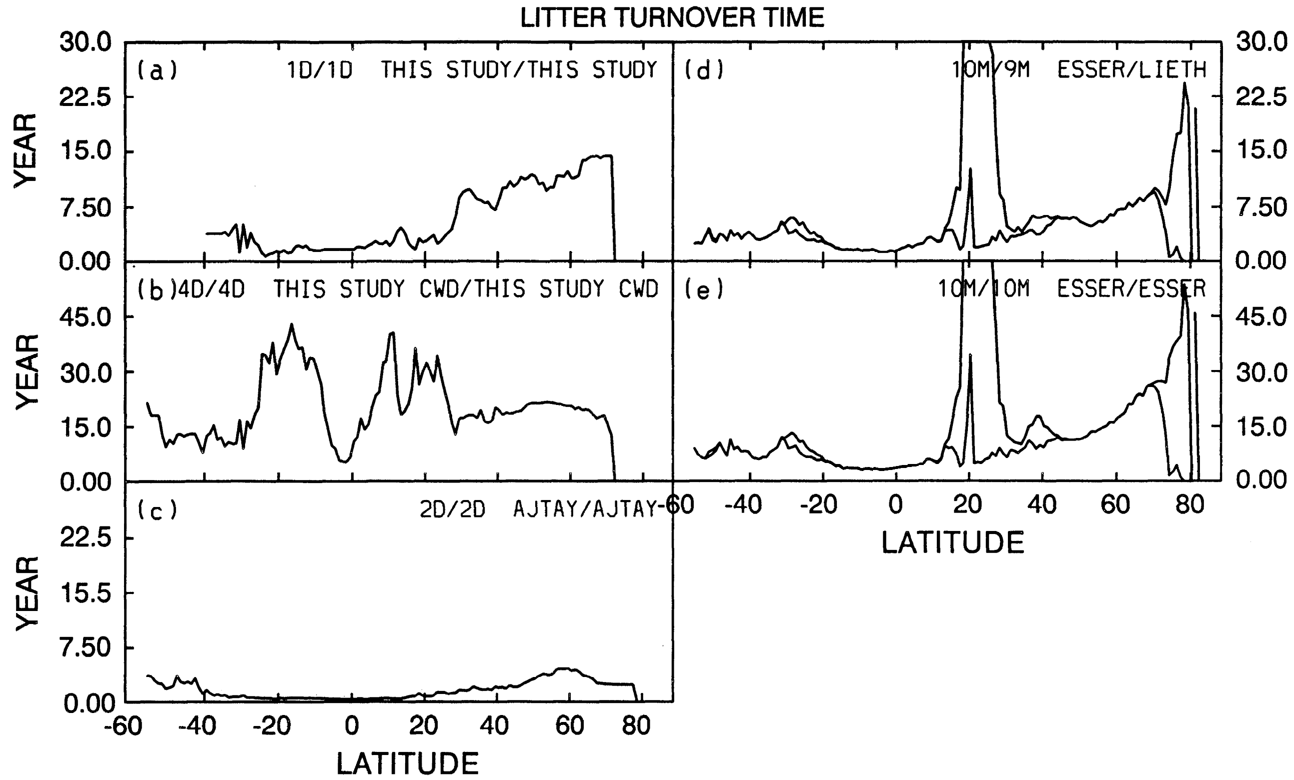

Figure 6. Mean zonal litter turnover time estimated from pool divided by production: a) 1D/1D, this study, pool and production from measurement compilation; b) 4D/4D, this study, CWD pool and production based on *Harmon and Hua* [1991]; c) 2D/2D, pool and production ecosystem composites from *Ajtay et al.* [1979]; d) 10M/9M, pool from *Esser et al.* [1982] and production from *Lieth* [1975]; e) 10M/10M, pool and production from *Esser et al.* [1982]. Light lines are values using models directly; heavy lines are the same except deserts are set to zero.

times (Figures 6d and 6e). As a matter of fact, subtropical and boreal turnover times appear to be anomalously large.

Zonal mean turnover times from the compiled measurements (Figure 6a) show tropical values similar to others, <1 yr, and a sharp rise north of 30°N to ~8 yr and a gently sloping plateau to ~15 years at 75°N. This pattern is underlain by generally homogeneous values across longitudes. Because this case is underestimating production (unrepresented ecosystems and only aboveground production) as well as pools (unrepresented ecosystems), it is difficult to interpret Figure 6a which represents a global mean of ~5 years.

6. Uncertainties

As outlined in the introduction, many uncertainties associated with estimates of litter production and pools influence estimates of the size, distribution, and composition of litter fields. In particular, uncertainties and biases arise from the following: (1) uncertainties inherent in measurements, (2) identification of measured components such as leaf and wood, (3) natural spatial and seasonal variability of production and pools, and (4) identification of ecosystems represented in the measurements.

6.1. Ecosystem Representation

Data gaps in the representation of ecosystems in the measurement data set include xeromorphic formations and non-wooded grasslands for both production and pools (Table 4b). In addition, shrublands, wooded grasslands, temperate evergreen seasonal forests, sclerophyllous forests and woodlands, boreal woodlands, and subtropical dry woodlands are not represented in the litter pool compilation. Forests and woodlands, characterized by large litter production and pools, are better represented than other ecosystems. However, desert, equal to 12% of the ice-free land surface, is narrowly defined in the vegetation data set by the absence of vegetation and additional arid ecosystems occupy another ~20% of the land. Carbon fluxes and pools in arid lands are understood to be small on a per-square-meter basis. Nevertheless, results of this study indicate that because of their large area, treatment of arid lands influences the magnitude and distribution of litter carbon pools. Results also show that some climate-based regression models overestimate litter pools and soil respiration in arid environments. This problem may not be easily solved since definitions and distributions of arid lands from various authors exhibit discrepancies that are difficult to reconcile [*Matthews*, 1983; *DeFries and Townshend*, 1994].

The scarcity of site information for reported measurements, including vegetation descriptions and locale, introduces uncertainty into the association of ecosystem measurements with the vegetation types in the data set used to extrapolate the measurements. Including more complete site descriptions, with the measurement results will reduce such uncertainties.

6.2. Litter Composition and NPP Allocation

Analysis of the new measurement compilation reveals that only ~25% of the litter measurements report both leaf and total fine production and even fewer distinguish woody production

(Table 4b). Furthermore, the present study highlights unresolved discrepancies in the size, distribution, and relative contribution of herbaceous and woody litter for some production totals.

The composition of litter production depends on the allocation of NPP among plant components (leaf, wood), and locations (aboveground and belowground). The physiochemical composition of litter production, in turn, determines decomposition dynamics and the resulting composition and mobility of litter pools [*Melillo et al.*, 1982]. In many models, allocation of NPP to plant components is prescribed (e.g., CASA [*Potter et al.*, 1993], DEMETER [*Foley*, 1994], SLAVE [*Friedlingstein et al.*, 1996]). These allocations are known to vary among ecosystems, and within ecosystems in response to interannual climate variations. *Vogt et al.* [1986] report that organic matter turnover in forests can vary by a factor of three when computed with and without fine roots (i.e., underground production).

Integration of measurements of belowground productivity with the measurement compilation will further quantify the role of underground components and processes. Such data include those presented by *Ruimy et al.* [1994], who report ratios of below-to-aboveground NPP for a large number of ecosystems. The work of *Raich and Nadelhoffer* [1989] quantifying belowground carbon allocation using measurements of aboveground litterfall and SR complements this goal. Their results indicate that the ratio of belowground C allocation to aboveground litterfall decreases as litterfall increases, i.e., the relative importance of belowground allocation varies with climate and ecosystem.

6.3. Coarse Woody Detritus

The initial global estimate of the CWD pool presented here is 150 Pg dm, about equal to the fine litter pool. Estimates of production and pool size have been hindered by the scarcity of measurements resulting from the difficulty of accomplishing such field studies [*Harmon et al., 1986, 1993*]. The probability of measuring a large number of representative ecosystems is very small. However, techniques developed by *Harmon et al.* [1986, 1993], and *Harmon and Hua* [1991] model CWD production and pools from standing live wood biomass and estimates of normal and catastrophic mortality. Because the results are highly dependent on the initial biomass distribution underlying the model, an exhaustive compilation of biomass measurements will increase confidence in this estimate.

6.4. Soil Respiration and Root Respiration

Techniques to estimate global litter production rarely include belowground processes, which can account for 30-50% of the total and vary among ecosystems. The SR-RR approaches presented here, which rely on isolating the contribution of root respiration to total soil respiration to arrive at an indirect estimate of litter production, are sensitive to assumptions of RR:SR ratios for ecosystems; these ratios are difficult to confirm from measurements [*Nakane et al.*, 1983; *Peterjohn et al.*, 1993]. An alternative is to use root:shoot or above:belowground relationships to estimate underground biomass indirectly, relying on the biomass compilation suggested for improving the CWD estimate or above:below ratios for NPP [*Ruimy et al.*, 1994]. Finally, although the difference between root respiration and soil respiration is dominated by the current year's litter production and decomposition, SR does include a contribution from decomposition of older litter (>1 year old) and SOM. Therefore, the current estimates based on SR may overestimate litter production by ~10% [*Dorr and Munnich*, 1989; *Trumbore*, 1993; *Schimel et al.*, 1994].

6.5. Anthropogenic Influences

Cultivated lands are not included in the present study, primarily to allow comparison with other studies that reflect natural vegetation conditions. Globally, permanent agricultural activities have replaced native vegetation on about 18×10^{12} m^2, or ~13% of the ice-free land, concentrated primarily in northern mid-latitude zones [*Matthews*, 1984]. Such conversion primarily impacts litter pools and biomass pools; the character of agricultural impacts on NPP and litter production is more controversial [*Ruimy et al.*, 1994] but probably less important.

7. Conclusions and Perspectives

The measured and modeled litter data presented here are designed to validate and/or parameterize litter dynamics and NPP allocation in ecosystem models. This study employs an integrated approach to estimating related litter pools and production, using a variety of data-based and modeled-based techniques. By including spatial distribution, magnitude and composition of litter, along with numerous measurements of production, pools, and turnover times, the approach is beginning to yield compositional and distributional constraints on modeled litter fields and NPP allocation. In addition, these results suggest that litter production and therefore NPP probably lie in the lower range of published estimates, ~90 Pg dm/yr.

The analysis includes direct and indirect, or proxy, estimates of litter production and pools from which steady-state turnover times are estimated. Proxies for litter production include NPP, the major input to litter production, and SR-RR, the major output of litter production. While measurements and most direct modeling approaches generally include only aboveground production, the SR-RR approaches have the advantage of encompassing both aboveground and belowground component.

Despite the large body of published litter measurements for individual sites, there are few global data available with which to compare these results. In addition, although ecosystem models characterize the composition and dynamics of inputs, decay, and transfers of litter materials among pools of organic matter in litter and soils, the definition of pools is often vague, and distributions and characteristics of modeled litter fields are rarely presented. Information on these parameters is often insufficient to diagnose causes underlying the differences among fields from various models. and global similarities often obscure regional, ecosystem, and compositional differences.

More than 1100 litter measurements from existing compilations have been integrated into a standard format from which estimates of total and leaf litter production, and litter pools, have been computed (Table 4). These measurements reflect aboveground production. Ecosystem coverage varies considerably, although larger litter producers, such as forests and woodlands, are better represented than are shrublands and grasslands. In addition, most litter production (60-80%) in these wooded ecosystems is aboveground so that the measurement data capture the bulk of production. However, the representation of ecosystems in the litter measurement data set shows large gaps (Table 4b). Because the composition and turnover time of litter pools depends partly on the allocation of NPP among plant components and the complex of litter components that are shed, better characterization of the woody litter component in both production and pools is crucial to improving allocation schemes in ecosystem models.

Historically, litter production has been estimated at 50-130 Pg dm/yr with most estimates between 90 and 120 Pg dm/yr (Table 1b). It is probable that some of the range is due to differences in the fields themselves. Aboveground fine litter production in the wooded ecosystems represented in the measurements is 39 Pg dm/yr. This value may approach 90-110 Pg dm/yr with the inclusion of unrepresented ecosystems and belowground production. Results presented here suggest that litter production, and NPP, are in the lower end of the 90-120 Pg range. Production values for individual ecosystems derived from the measurements are generally lower than those from other techniques, most likely because the measurements reflect aboveground production although this could not be confirmed. The measurement data indicate that ~65-70% of production is leaf material and the remainder is fine woody material.

Approaches to estimate global litter production rarely include belowground production, which can account for a substantial fraction of the total, and which increase with increasing aridity and herbaceous dominance. We present here a simple approach of isolating RR from SR to approximate total fine litter production. The SR distributions, derived using ecosystem composites and climate, are estimated to be 145 and 160 Pg dm/yr, respectively; RR is 52 and 60 Pg dm/yr, respectively; and global values for litter production are 93 and 100 Pg dm/yr, respectively. Despite the simplicity of the technique, it has the advantage of representing total production and therefore of providing bounds on NPP and litter production.

Estimates of the global litter pool, from a variety of extrapolation techniques and models, range from 100 to 400 Pg dm (Table 1a). As with production, some of the variation is likely due to differences in the definition of litter since characteristics of the litter pool are often undefined. Few model estimates explicitly include coarse woody detritus or underground detritus, and measurements of litter pools exhibit the same scarcity. Using the measurements, the global fine litter pool is estimated at ~135 Pg dm. While this represents ecosystems occupying only about 50% of the world's ice-free land surface, it includes most ecosystems with substantial litter pools. Addition of the remaining ecosystems may increase the total to ~160 Pg dm. The measurements indicate that some tropical regions have larger litter pools than expected.

The CWD pool and production estimates are very uncertain but initial results presented here suggest that CWD production is ~12 Pg dm annually and the CWD pool may be of the order of 150 Pg dm, about equal to the fine litter pool. While this pool does not participate in short-term variations in production and decomposition, it can affect carbon dynamics on decadal time scales.

This study highlights internal inconsistencies between pool and production composites of a commonly referenced source [*Ajtay et al.*, 1979], as evidenced by the very short mean global litter turnover time of 1.4 years; turnover times of tropical ecosystems are ~0.5 years, consistent with other results. However, most other ecosystems, including temperate and boreal forests and woodlands, exhibit unrealistically short turnover times of 3-6 years.

In general, ecosystem-based extrapolations of production and pools have the disadvantage of producing unrealistically abrupt boundaries instead of smooth gradients. Climate-based regressions reflect ecologically reasonable gradients but tend to overestimate values in unvegetated deserts and in substantial areas of xeromorphic formations. For example, ~10% of the global litter pool of *Esser et al.* [1982] occurs in unvegetated desert locations (Figure 5d). Similarly, for the climate-based SR distribution, 10% of the SR total occurs in deserts (Plate 3b). Smaller effects occur in other arid, non-desert regions.

Systematization of the enormous number of litter measurements already published is necessary to validate and parameterize litter dynamics and NPP allocation in ecosystem models. We have begun to integrate and reconcile 3 compilations of litter measurements (this compilation, E. Holland and J. Sulzman's (NCAR) and W. M. Post's (Oak Ridge National Laboratory [*Matthews et al.*, 1997]).

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